EVALUATION OF GROWTH, SURVIVAL, AND RECRUITMENT OF CHINOOK SALMON IN SOUTHEAST ALASKA RIVERS

By

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Abstract

Recent reductions in the run sizes of Chinook Salmon *Oncorhynchus tshawytscha* in Southeast Alaska have resulted in social and economic hardships within the region. Pacific salmon year-class strength may be determined by size-selective processes during the early marine phase of their life cycle; however, the relative importance of growth during freshwater and marine residence in determining recruitment success is unknown. A scale-based retrospective analysis was conducted to examine the effects of freshwater and annual marine growth and early marine conditions on survival to reproductive maturity for female Chinook Salmon by brood year (BY) in the Taku (BYs 1979 – 1985, 1990 – 1999, 2002 – 2004) and Unuk (BYs 1981 – 1983, 1986 – 1988, 1994 – 2003, 2005 – 2006) rivers. First-year marine growth was positively related to survival and total return for Chinook Salmon stocks from both systems. Growth during freshwater residence (i.e., size-at-ocean entry) was not related to survival or total return of either stock. In addition, there was a positive relationship between marine survival of Unuk River Chinook Salmon and sea-surface temperatures in Upper Chatham Strait, Icy Strait, and Auke Bay Monitor ($P = 0.04$) during early marine residence. The results of my research highlight the importance of growth and marine conditions during the first year at sea in determining the survival of Chinook Salmon in Southeast Alaska and suggest that current declines in run sizes and survival of stocks within this region may be the attributed to poor growth conditions or growth during early marine residence.

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General Introduction

Growth is an important process that influences the reproductive success of fish (Candolin and Voigt 2001; Wacker et al. 2012). Fecundity and egg size are positively related to female spawner body size for most fishes (Beacham et al. 1985; Manzer and Miki 1986; Dickerson et al. 2002). In addition, large body size enables individuals to secure high quality habitats, which may lead to fitness advantages over smaller conspecifics (Candolin and Voigt 2001; Wacker et al. 2012). For instance, large Threespine Sticklebacks *Gasterosteus aculeatus* were able to defend larger territories and encountered females at higher rates than smaller individuals in the population (Candolin and Voigt 2001). Both biotic and abiotic processes regulate growth in fish, with temperature and food availability being of primary importance (Groot et al. 1995). Fish are poikilotherms; therefore, the metabolic rates of fish are regulated by ambient temperatures. In general, fish growth rates increase until an optimum temperature is reached (Groot et al. 1995); once this temperature is exceeded, growth rates decline due to high basal metabolic costs (Wootton 1998). Biotic factors, such as quality and quantity of food resources, also affect somatic growth rates (Wootton 1998), as illustrated by a positive relationship between the abundance of drifting invertebrates and juvenile Coho Salmon *Oncorhynchus kisutch* growth rates (Rosenfeld et al. 2005). Further, the nutritional quality of prey resources may also affect growth rates (Wootton 1998). For example, in the western Gulf of Alaska, variations in Walleye Pollock *Gadus chalcogrammus* growth rates have been attributed to regional differences in zooplankton species composition (Wilson et al. 2013).

In addition to reproductive success, growth may also influence survival due to size-selective mortality, with large-bodied fish exhibiting higher survivorship when facing predators,

extreme environmental conditions, or periods of low food availability (Sogard 1997; Hurst 2007). Large body size reduces the risk of predation in two ways. First, large size physically prevents predation due to gape limitations of predators. Second, swimming ability is positively related to body size; therefore, larger fish can swim faster to escape potential predators than smaller individuals (Sogard 1997). Large-bodied fish also have a survival advantage over smaller conspecifics during periods of low food availability due to the allometric scaling of metabolic requirements; larger individuals need to expend less energy per unit body mass on basal processes than smaller fish (Thompson et al. 1991; Sogard 1997; Wootton 1998; Schultz and Conover 1999; Biro et al. 2004; Hurst 2007). Finally, larger fish have a lower gill surface area relative to body mass, which may increase survival when experiencing extreme environmental conditions (Sogard 1997; Bjerknes et al. 1992). For example, Bjerknes et al. (1992) found that small Atlantic Salmon parr *Salmo salar* had lower osmoregulatory abilities and higher rates of mortality than larger individuals when exposed to stepwise increases in salinity levels. Therefore, growth may regulate survival of fish groups that experience high rates of predation and extreme environmental conditions.

Salmon are susceptible to size-selective mortality throughout their freshwater and marine residence. In freshwater, predation is thought to be an important cause of mortality in Pacific salmon, with juveniles being exposed to a suite of potential predator groups, such as mammals, birds, and other fishes (Peterson 1982; Wood 1987; Quinn 2005). In addition, the physiological stress associated with overwintering in freshwater may result in high rates of size-mediated mortality (Hurst 2007; Brown et al. 2011). For example, pre-winter body size and condition were positively related to overwinter survival in several species of salmonids (Smith and Griffith 1994; Meyer and Griffith 1997; Huusko et al. 2007). Size-selective processes are also thought to

mediate salmon mortality while in the ocean. The critical size, critical period hypothesis proposes that salmon mortality in the ocean is concentrated in two distinct periods during early marine residence (Beamish and Mahnken 2001). The first period of high mortality is size-mediated and occurs shortly after smolts enter the ocean. Smolting is an osmotically stressful process that may lead to reduced predator avoidance and high mortality when entering predator-rich coastal environments (Handeland et al. 1996; Dieperink et al. 2002). Recent studies indicate that smolt body size at ocean entry is positively related to marine survival for Atlantic and Pacific salmon (Kallio-Nyberg et al. 2004; Jutila et al. 2006; Antonsson et al. 2010; Murphy et al. 2013). Therefore, smolts that do not reach a "critical size" are more likely to suffer predation-based mortality soon after entering the ocean than smaller individuals. The second period of high mortality for Pacific salmon in the ocean occurs during the first marine winter (Beamish and Mahnken 2001; Beamish et al. 2004). Similar to freshwater, the overwintering period in the marine environment is physiologically stressful; as a result, individuals that fail to store sufficient energy reserves during their first marine summer and fall may deplete their energy stores and suffer starvation-induced mortality during their first marine winter (Beamish and Mahnken 2001; Beamish et al. 2004). Therefore, if conditions are poor for growth and size-selective mortality is high, size-mediated mortality in freshwater and marine environments may regulate brood year-class strength of Pacific salmon (Bradford 1995; Sogard 1997; Beamish and Mahnken 2001).

Climate plays an important role in shaping marine ecosystems, which in turn, may affect Pacific salmon production directly through changes in water temperature and indirectly through changes in bottom-up processes (Mueter et al. 2002; Edwards and Richardson 2004; Seo et al. 2006; Noakes and Beamish 2009; Petrosky and Schaller 2010; Doney et al. 2012). Multiple

studies indicate significant relationships between sea-surface temperatures (SST) and Pacific and Atlantic salmon survival (Koslow et al. 2002; Mueter et al. 2002, 2005; Logerwell et al. 2003; Kallio-Nyberg et al. 2004; Stachura et al. 2014; Miller et al. 2014). For instance, regional SSTs influenced survival rates for both northern (i.e., Alaska) and southern stocks (i.e., British Columbia and Washington) of Pacific salmon (Mueter et al. 2002). Climate may also affect the survival of Pacific salmon indirectly through changes in the timing and availability of primary and secondary production (Edwards and Richardson 2004; Petrosky and Schaller 2010). Climate is dynamic and can change directionally or oscillate between varying regimes, both of which may alter trophic relationships (Francis et al. 1998; Hare and Mantua 2000; Mantua and Hare 2002). Variations in long-term abundance trends of Pacific salmon from large regions in the North Pacific Ocean have tracked changes in large-scale climate indices such as the Pacific Decadal Oscillation (PDO; Mantua et al. 1997; Hare and Mantua 2000) and the Aleutian Low Pressure Index (ALPI; Beamish and Bouillon 1993). Thus, the non-static nature of climate and its regulation of the processes that influence recruitment success may explain long-term fluctuations in the abundance of highly valued species such as Chinook Salmon *Oncorhynchus tshawytscha*.

Chinook Salmon is the largest and least abundant species of Pacific salmon and has a spawning distribution that ranges from south-central California to Kotzebue Sound, Alaska, in North America and Hokkaido, Japan, to the Anadyr River, Russia (Healey 1991; Quinn 2005). Certain traits, such as anadromy and semelparity, are common to Chinook Salmon throughout their range (Quinn 2005). However, Chinook Salmon stocks exhibit diverse life-history strategies due to specialized adaptations to local environments, but in general can be classified into two life-history types based on extent of freshwater rearing (Healey 1991; Quinn 2005).

Ocean-type Chinook Salmon do not rear in freshwater for extended periods, and instead migrate to the ocean soon after emerging from the gravel. This life-history strategy is only found at the southern end of their spawning distribution (i.e., south of 56° latitude). In contrast, stream-type Chinook Salmon rear in freshwater for 1-2 years prior to migrating to the ocean. While stream-type Chinook Salmon are found throughout their spawning range, they are more common in northern extent of their distribution (i.e., Alaska).

In Alaska, Chinook Salmon spawning migrations occur in the spring and summer, while spawning takes place in the late summer or fall (Quinn 2005; Hendrich et al. 2008; McPherson et al. 2010). Chinook Salmon spawn in a wide range of habitats, but in general prefer areas with high subgravel flow (Healey 1991; Quinn 2005). Female spawners deposit eggs into redds where, after being fertilized by males, the embryos incubate in the gravel overwinter. Embryos hatch the following spring, and the majority of parr spend one year in freshwater prior to immigrating to the ocean between April and July as age-1 smolts (Hendrich et al. 2008; McPherson et al. 2010). After entering the marine environment, Alaska Chinook Salmon make extensive, seasonal offshore migrations (Myers et al. 2009). In Southeast Alaska (SEAK), the extent of oceanic migrations varies by stock, with some rearing within the waters of SEAK and British Columbia and others migrating into the Gulf of Alaska and the Bering Sea (Der Hovanisian et al. 2011). Chinook Salmon spend 2-5 years feeding in the marine environment prior to returning to their natal stream to spawn (Hendrich et al. 2008; McPherson et al. 2010). Variations in life-history strategies exhibited by stocks across the state may explain regional differences in the recruitment success of Chinook Salmon.

The productivity (return per spawner) of Chinook Salmon stocks has long displayed considerable temporal and regional variability within Alaska. Recently, declines in productivity

have been widespread across the state, which have prompted researchers to identify the cause of these declines (ADF&G Chinook Salmon Research Team 2013; Schindler et al. 2013). Due to the importance of size-mediated processes in determining recruitment success, the factors driving recruitment failure may be uncovered by studying long-term variations in growth and their relation to productivity. One useful way to study long-term changes in abundance and recruitment is scale-based retrospective analyses.

Scale-based retrospective analyses have been used to study long-term trends in growth and their relationship to climate, survival, and productivity in salmon (Healey 1982; Holtby et al. 1990; Crozier and Kennedy 1999; Friedland et al. 2000; Beamish et al. 2004; Farley et al. 2007; Ruggerone et al. 2007, 2009; Cross et al. 2008). Scale formation (i.e., circulus spacing and formation rate) is positively related to somatic growth rate (Fisher and Pearcy 2005; Walker and Sutton 2016) and can be used as an index of growth in salmon (Ruggerone et al. 2007; McCarthy et al. 2008; Hogan and Friedland 2010). Further, scale formation can be correlated to recruitment benchmarks (e.g., total return, productivity, etc.) to determine how growth rates influence survival throughout the life cycle of Pacific salmon (Fisher and Pearcy 2005; McCarthy et al. 2008; Hogan and Friedland 2010). For example, circulus spacing indicates that early marine growth influences survival in Atlantic Salmon *Salmo salar* (Friedland et al. 2000), Sockeye Salmon *O. nerka* (Ruggerone et al. 2007), Coho Salmon *O. kisutch* (Beamish et al. 2004), and Pink Salmon *O. gorbuscha* (Moss et al. 2005; Cross et al. 2008). Ruggerone et al. (2007) found a positive correlation between the run sizes of Sockeye Salmon from western and central Alaska and scale growth during the first two years at sea. Scale-based retrospective analyses have also been used to examine the influence of freshwater growth on productivity of Chinook Salmon from tributaries of the Yukon and Kuskokwim rivers (Leon 2013) and on the pre-fishery

abundance of Atlantic Salmon from the Drammen River, Norway (McCarthy et al. 2008). Neither study found a significant effect of freshwater growth on recruitment, but previous research indicates freshwater growth may be important because it positively correlated with first year marine growth in Chinook Salmon (Ruggerone et al. 2009; Leon 2013). Therefore, examining time series of scale growth patterns may lend insights into the factors that influence survival, productivity, and abundance of Chinook Salmon.

While size-selective processes are thought to influence the brood-year recruitment success of Pacific salmon, there role in current recruitment declines of Chinook Salmon in SEAK is unknown. Chapter one of this thesis characterizes the influence of freshwater and marine annual growth in determining the recruitment success of Taku and Unuk River Chinook Salmon. The second chapter examines the relative influence of biotic and abiotic factors on the freshwater overwinter survival and smolt production of Unuk River Chinook Salmon. Chapter 3 investigates the influence of early marine conditions and smolt body size on the marine survival of Unuk River Chinook Salmon. Overall, this research provides insights into the factors potentially responsible for the reduced runs sizes and survival of stocks across the region and can be used to guide future research in this area.

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Chapter 1: Evaluation of growth, survival, and recruitment of Chinook Salmon in Southeast Alaska rivers[1]

Abstract

Chinook Salmon *Oncorhynchus tshawytscha* brood-year (BY) strength may be determined by size-selective processes that occur during early marine residence; however, the relative importance of freshwater versus marine growth in determining recruitment success is unknown. A scale-based retrospective analysis was conducted to examine the relative effects of freshwater and marine growth on survival to the age of reproduction, determine if growth dependency between adjacent growth zones was present, and analyze the influence of smolt body size on survival to reproductive maturity for female Chinook Salmon by BY in the Taku (BYs 1979 – 1985, 1990 – 1999, 2002 – 2004) and Unuk (BYs 1981 – 1983, 1986 – 1988, 1994 – 2003, 2005 – 2006) rivers. First-year marine growth (SW1) was positively related to survival and total return for Chinook Salmon stocks from both systems. In the Taku River, growth during the third year at sea was positively related to marine survival. Growth during freshwater residence (i.e., size-at-ocean entry; FW1) was not related to the survival or total return of either stock. Annual growth of Taku River Chinook Salmon was correlated with previous growth through the second year at sea (SW2; FW1 versus SW1 [r = 0.11]; SW1 versus SW2 [r = 0.10]); however, no correlations were detected between adjacent growth zones of Unuk River fish (FW1 versus SW1 [r = -0.01]; SW1 versus SW2 [r = 0.01]). Positive skew and low variability of freshwater growth distributions suggested that smolts experienced size-selective mortality during early marine residence. These findings suggest that current regional declines in Chinook Salmon abundance are likely attributed to changes in growth conditions during the first year at sea.

[1] Graham, C. J., T. M. Sutton, M. V. McPhee, M. D. Adkison, and P. J. Richards. 2016. Evaluation of Growth survival and recruitment of Chinook Salmon in Southeast Alaska. Prepared for submission to Transactions of the American Fisheries Society.

Introduction

Chinook Salmon *Oncorhynchus tshawytscha* are valued as social, cultural, and economic resources in Southeast Alaska (SEAK; Der Hovanisian et al. 2011). For example, Chinook Salmon are harvested in commercial, sport, and subsistence fisheries throughout the region (Der Hovanisian et al. 2011). Commercial fisheries target Chinook Salmon with a variety of gear types (e.g., drift gill nets, purse seines, etc.), but the troll fishery harvests the majority of the commercial catch of this species. Multiple Chinook Salmon stocks in SEAK are also harvested via in-river commercial fisheries in Canada (e.g., Taku and Stikine rivers). However, recent declines in stock abundances have led to harvest restrictions and, consequently, regional reductions in sport fish landings and commercial harvests (ADF&G Chinook Salmon Research Team 2013). Because reduced harvests may cause social and economic hardships for multiple user groups, it is important to understand the factors contributing to the current declines in Chinook Salmon stocks across SEAK.

Previous research indicates that salmon abundance is mediated by size-dependent mortality, with the time period during freshwater and early marine residence being critical for influencing survival patterns and, ultimately, recruitment to the spawning stock (Beamish and Mahnken 2001; Farley et al. 2007). The critical size, critical period hypothesis proposes that Pacific salmon year-class strength is determined during two distinct periods of high mortality during the first year of marine residence (Beamish and Mahnken 2001). The first period of high mortality is driven by size-dependent predation shortly after smolts enter the marine environment (Pearcy 1992). Smoltification is an osmotically stressful process that may lead to reduced predator avoidance and high mortality when entering predator-rich coastal environments

(Handeland et al. 1996; Dieperink et al. 2002). Large smolt body size may reduce the risk of predation in two ways (Sogard 1997). First, large body size may physically prevent predation due to gape limitations of predators (Sogard 1997; Juanes et al. 2002; Dörner and Wagner 2003). Second, swimming ability increases with body size; therefore, large smolts can swim faster to escape potential predators than smaller-bodied members of their cohort (Juanes 1994). Because body size at ocean entry has been found to influence the marine survival of Atlantic Salmon *Salmo salar* (Jutila et al. 2006) and Pacific salmon (Woodson et al. 2013), high growth during freshwater residence may increase survival during the first period of high mortality. The second period of high mortality is mediated by physiological processes and occurs during the first fall and winter at sea. The overwinter period in the marine environment is physiologically stressful; as a result, individuals that fail to store sufficient energy reserves during their first marine summer may deplete their energy stores and suffer mortality during their first fall and marine winter at sea (Beamish and Mahnken 2001; Beamish et al. 2004). Large-bodied fish are also thought to have a survival advantage during this period due to the allometric scaling of metabolic requirements which requires that large fish expend less energy per unit biomass on basal processes than smaller fish (Thompson et al. 1991; Sogard 1997; Schultz and Conover 1999; Biro et al. 2004). Because mortality is mediated by size-dependent processes during the first year at sea, rapid growth during freshwater and early marine residence may increase the survival of Pacific salmon. Therefore, if conditions are poor for growth and size-selective mortality is high, size-mediated mortality during the first marine year may reduce the brood year strength of Pacific salmon (Sogard 1997; Beamish and Mahnken 2001).

Climate plays a profound role in shaping the structure and function of marine ecosystems, which in turn, may affect Pacific salmon growth and survival directly through changes in water

temperature and indirectly through changes in bottom-up processes (Mueter et al. 2002; Edwards and Richardson 2004; Seo et al. 2006; Noakes and Beamish 2009; Petrosky and Schaller 2010; Doney et al. 2012). The survival of Pacific salmon has been linked to variations in sea-surface temperatures at regional and basin-wide scales (Mueter et al. 2002, 2005; Burke et al. 2013). For instance, regional sea-surface temperatures influenced the survival rates of northern (i.e., Alaska) and southern stocks (i.e., British Columbia and Washington) of Pacific salmon (Mueter et al. 2002). Climate may also affect the survival of Pacific salmon indirectly through changes in the timing and availability of primary and secondary production (Edwards and Richardson 2004; Petrosky and Schaller 2010). For example, the match-mismatch hypothesis proposes that variability in the recruitment success of fishes may be related to spatial and temporal overlap of the availability of biological production and key life-history events (e.g., timing of outmigration; Cushing 1990; Tomaro et al. 2012). Due to the importance of growth and climate in influencing the survival patterns of Pacific salmon, the factors driving the current recruitment failures of Chinook Salmon in SEAK may be uncovered by studying long-term variations in growth and their relation to productivity and survival. One useful way to study long-term changes in growth of fishes is scale-based retrospective analysis.

Scale-based retrospective analyses have been used to study long-term trends in growth and their relationship to climate, survival, and productivity in both Pacific and Atlantic salmon (Healey 1982; Holtby et al. 1990; Crozier and Kennedy 1999; Friedland et al. 2000; Beamish et al. 2004; Farley et al. 2007). Scale formation (i.e., circulus spacing and formation rate) is proportionally related to somatic growth and therefore can be used as an index of growth in salmon (Fisher and Pearcy 2005; Ruggerone et al. 2007; McCarthy et al. 2008; Hogan and Friedland 2010; Walker and Sutton 2016). Further, scale formation can be correlated to

recruitment benchmarks (e.g., total return, productivity, etc.) to determine how growth rates influence survival throughout the life cycle of Pacific salmon (Fisher and Pearcy 2005; Ruggerone et al. 2007; McCarthy et al. 2008; Hogan and Friedland 2010; Leon 2013). For example, Ruggerone et al. (2007) used scale- formation rate to determine that variability in the abundance of Bristol Bay and Chignik Sockeye Salmon *O. nerka* stocks was influenced by growth during the first two years at sea. Therefore, examining time series of scale-growth patterns may lend insights into the factors influencing the survival, productivity, and abundance of Chinook Salmon in SEAK.

The goal of the current study was to determine how annual growth influences the recruitment success of Chinook Salmon in SEAK. To accomplish this goal, time series of freshwater and marine growth patterns were constructed and correlated to a series of recruitment benchmarks (i.e., total return, productivity, marine survival) for two regionally important Chinook Salmon stocks in SEAK (i.e., Taku and Unuk river Chinook Salmon stocks). The specific objectives of this study were to: 1) characterize the importance of freshwater and annual marine growth in determining the recruitment success of Chinook Salmon in SEAK; 2) determine if growth dependency was present in Chinook Salmon in SEAK; and 3) investigate the relationship between smolt body size and survival to reproductive maturity by brood year (BY). This study provides a region-wide perspective on potential linkages between growth and survival patterns, relationships in fresh and marine waters, and trends in abundance relative to recruitment for Chinook Salmon in SEAK.

Methods

Study sites

This study was conducted on Chinook Salmon captured in the Taku and Unuk rivers in SEAK (Figure 1.1). The Taku River is a large, glacially influenced river system originating in the Stikine Plateau of northwestern British Columbia (Der Hovanisian et al. 2011). This river flows approximately 300 km through mountainous terrain before draining into Taku Inlet 30 km east of Juneau, Alaska. The glacial nature of the Taku River results in highly turbid mainstem waters. In contrast, most tributaries of the Taku River are clear water with little glacial till. This pristine watershed is large, encompassing an area over 17,000 km^2, and is an important producer of all five North American species of Pacific salmon. The Unuk River is a large, glacially fed river that originates in northern British Columbia and flows through the glacially forged Misty Fjords National Monument, which has been designated a federally protected wilderness area, before draining into Behm Canal northeast of Ketchikan, Alaska (Der Hovanisian et al. 2011). Similar to the Taku River, the Unuk River is characterized by highly turbid mainstem waters and clear-water tributaries. The Unuk River is approximately 129 km in length, and drains an area that is approximately 3,885 km^2. In addition, the Unuk River supports healthy runs of all five species of North American Pacific salmon.

The Taku and Unuk rivers were chosen for this study for multiple reasons. Both rivers are important salmon producers within SEAK. On average, the Taku River has the largest Chinook Salmon run in the region, with mean run sizes of 50,000 large (> 660 mm) fish per year (Der Hovanisian et al. 2011). The Unuk River is the fourth largest producer of Chinook Salmon in SEAK, with annual runs of approximately 5,500 large fish (Der Hovanisian et al. 2011). Taku

and Unuk river Chinook Salmon stocks exhibit diverse ecological and genetic characteristics, such as distinct marine-rearing locations (Der Hovanisian et al. 2011; ADF&G Chinook Salmon Research Team 2013). After emigrating to the ocean, juvenile Chinook Salmon from the Taku River are thought to reside in coastal waters prior to migrating offshore, where they make seasonal migrations in the Gulf of Alaska and the Bering Sea for the remainder of their ocean residence (McPherson et al. 2010). In contrast, Chinook Salmon from the Unuk River rear primarily in nearshore waters of SEAK and British Columbia, and most do not make extensive offshore migrations to the Bering Sea (Der Hovanisian et al. 2011). Finally, the Unuk River was selected for this study due to the proposed development of Kerr-Sulphurets-Mitchell mine (KSM), which is a proposed transboundary, open-pit mine located on Sulphurets Creek in northern British Columbia, a tributary of the Unuk River. As planned, KSM will be similar in scale to the proposed Pebble Mine (Canadian Environmental Assessment Agency 2014). The location of the proposed KSM dam and the long-term storage of waste threatens spawning and rearing habitat for Chinook Salmon and other Pacific salmon stocks. It is estimated that approximately 83% of Chinook Salmon from the Unuk River spawn downstream from the Canadian border (Pahlke et al. 1995). The inclusion of these rivers in this evaluation will allow for the characterization of the relationship between annual growth and recruitment success for regionally important salmon stocks that experience distinct freshwater and marine rearing locations.

Scale samples

A time series of freshwater- and marine-growth patterns for female Chinook Salmon from the Taku (BYs 1979 – 1986, 1990 – 2000, 2002 – 2008) and Unuk (BYs 1976, 1978 – 1989, 1993 –

2006) rivers was constructed by brood year using scales collected by the Alaska Department of Fish and Game (ADF&G). Chinook Salmon in both systems were sampled during spawning migrations using a variety of gear types (e.g., set gill nets, fish wheels, weirs, hook and line,) that varied by system and year. The ADF&G employs a multi-gear sampling method because experience has shown that the use a variety of gear types produces unbiased estimates of age, sex, and length composition for Taku and Unuk river Chinook Salmon (McPherson et al. 1997; Jones et al. 1998). In both systems, scales were collected from the preferred area: two rows above the lateral line between the posterior end of the dorsal fin and the anterior end of the anal fin (Hagen et al. 2001). Five scales were taken from each sampled fish and mounted on gummed scale cards for long-term storage. These scale samples were used to create acetate impressions, which were later analyzed in this study.

Of the fish sampled by ADF&G, only scales from female Chinook Salmon were analyzed, which is justified for several reasons (Leon 2013). First, female fish determine the maximum possible number of offspring through the number of eggs produced. Second, there is a strong linear relationship between female body size and reproductive potential (i.e., fecundity) in salmonids (Quinn 2005). In contrast, the relationship between body size and reproductive success in males is complicated by pronounced sexual dimorphism (e.g., kype, humped dorsal surface) that is formed during their spawning migration (Kinnison et al. 2003; Quinn 2005). Finally, female returns have a simpler age structure than males, resulting in fewer returning age classes and a simplified set of analyses. For example, male Chinook Salmon from both systems may return at ages 1.1 through 1.5, while female Chinook Salmon predominately return as age 1.3 and 1.4 fish (McPherson et al. 2010). Therefore, the inclusion of only female Chinook Salmon in this study reduced the number of age classes for analysis.

Scale reading

Scales had to meet the following criteria to be selected for analysis: 1) the scale's circuli, annuli, and focus were clearly defined; and 2) the scale was sampled from preferred area of the fish. Scales selected for analysis were digitized according to the semi-automated image analysis procedure outlined by Hagen et al. (2001). Scale images were captured using a high-resolution line camera (Screenscan® Microfiche Scanner, Salem Wisconsin) attached to an Indus 4601 microfiche reader and stored as Tagged Image File Format (TIFF) files with a resolution of 3352 x 4425 pixels. High-resolution images allowed the entire scale to be viewed and insured the accurate representation and measurement of intercirculi spacing. Digitized scale images were uploaded into ImagePro® 7.0 Image Analysis Program (Image-Pro Plus, Acton, Massachusetts), where the macro OtolithAnalysis was used to semi-automatically define annuli and measure circuli spacing for each scale. Once the digitized image was loaded into Image-Pro Plus, a reference line was established along the longest scale axis from the focus to the scale's edge. The scale reader marked all annuli along the reference line and OtolithAnlaysis flagged all circuli using edge detection algorithms. Because the accuracy of the edge detection algorithms varied with scale quality, the scale reader manually reviewed and edited each circuli placement. When all annuli and circuli were correctly marked, OtolithAnlaysis enumerated all annuli and circuli and measured intercriculi widths. The count and measurement data were then exported as a text file, which was subsequently exported and saved into Microsoft Excel.

Growth zones extracted from scales were defined using the following criteria. Freshwater growth (FW1) was the measured distance (mm) from the focus to the outermost edge of the first annulus (Figure 1.2). The first year of marine growth (SW1) was the measured distance between the last freshwater circuli and the annulus separating SW1 and the second year of marine growth

(SW2). Subsequent years of marine growth (i.e., SW3, SW4) were defined as the measured distance from the previous to the next annulus (Figure 1.2).

Recruitment benchmarks

Estimates relating to the recruitment success (e.g., abundance, total return, marine survival, productivity) of Chinook Salmon stocks from the Taku and Unuk rivers were obtained from ADF&G. In both systems, biological data such as age, sex, and length (ASL) data were collected during their annual stock assessment programs, which allowed escapement, survival, and marine harvest to be estimated (Hendrich et al. 2008; McPherson et al. 2010).

Currently, the spawning abundance of large ($\geq$ 660 mm mid-eye to tail fork [MEF]) and small ($<$ 660 mm) adult Chinook Salmon has been estimated using two-event mark-recapture experiments in both the Taku (1995 – present) and Unuk (1997 – present) rivers. In the Taku River, fish wheels and set gill nets (13.7-cm or 18.4-cm stretch mesh) were used to capture Chinook Salmon during the first event just below the Canadian border. All captured fish were sampled to determine the ASL composition of the in-river run. All fish that were not missing their adipose fin and determined to be in good condition were marked using solid-core spaghetti tags. A left upper operculum punch (0.63 cm in diameter) was also used as a secondary mark to assess tag retention rates. During the second event, Taku River Chinook Salmon were captured on the spawning grounds with a variety of gear types. Each captured fish was inspected for presence of a spaghetti tag, left upper operculum punch, and missing adipose fin. After mark inspection, ASL data were collected and a lower left operculum punch was used to prevent double sampling.

In the Unuk River, Chinook Salmon were marked after being captured with set gill nets (37 m long × 4 m deep, with 1.8-mm stretch mesh) in the lower portion of the river below the Canadian border for the first event. Methods for sampling and marking fish followed the same procedures as in the Taku River. In the second event, fish were visually examined for marks on the spawning grounds or after being caught with rod and reel, dip nets, and gill nets. In both systems, the abundance of large and small adult Chinook Salmon was estimated separately by the ADF&G using a modified Chapman-Petersen estimator (Seber 1982).

Prior to the onset of the two-event mark-recapture experiments, relative abundance was estimated suing aerial surveys during periods of peak spawning in major tributaries of the Taku and Unuk rivers. In both systems, relative abundance estimates from aerial surveys were converted into estimated spawning abundances, with expansion factors calculated from years when both aerial surveys and mark-recapture experiments were conducted (Unuk River [N = 7], Taku River [N = 13]).

Total return was calculated as the sum of estimated in-river run and marine harvest for 1.2 to 1.5 age fish within a given BY. Abundance by age class was estimated using the estimated abundance of small and large fish and size-composition data from the spawning ground surveys. The marine harvest of Chinook Salmon in regional commercial and sport fisheries was estimated following the methods described by Bernard and Clark (1996).

Marine survival was calculated as the ratio of BY total return and the estimated BY smolt abundance. The BY abundance of Unuk and Taku river smolts was estimated by the ADF&G using a two-event mark-recapture experiment using a modified Chapman-Petersen formula (Seber 1982; Weller and Evans 2012). In the first event, Chinook Salmon smolts were captured using minnow traps (420 mm long × 191 mm diameter, with 6-mm mesh) baited with salmon roe

in back eddies and major sloughs of the lower potions of the Taku and Unuk rivers during smolt outmigration from late March through early May (Hendrich et al. 2008; Weller and Evans 2012). All captured smolts $\geq$ 50 mm fork length (FL) that were not missing an adipose fin were implanted with a coded wire tag (CWT) and marked by excising their adipose fin for future identification. In the second event, adults were sampled on the spawning grounds when estimating the in-river abundance of mature Chinook Salmon.

Relationship between annual growth zones and recruitment benchmarks

To determine the influence of annual growth on survival to the age of reproduction, scale-growth patterns for the Taku and Unuk rivers were related to Chinook Salmon recruitment benchmarks (i.e., total return, productivity) using multiple regression analyses. Over the time series of scale growth patterns for the Taku River, the majority of BYs were sampled using set gill nets or fish wheels. Gear types may select for fish of different sizes (Wells et al. 2008); therefore, a Hotelling's T^2 test (Manly 1994) was used to compare the average growth zone distance for each annual growth zone (i.e., FW1, SW1, SW2, SW3, and SW4) for Taku River Chinook Salmon of the same age (i.e., age-1.3 or age-1.4 fish) and BY, collected with set gill nets and fish wheels. Results indicated that there were no statistically significant ($P < 0.05$) differences between any of the annual growth zones for either age-1.3 fish (BY 2003 [$P = 0.11$], 2004 [$P = 0.50$], and 2006 [$P = 0.42$]) or age-1.4 fish (BY 2003 [$P = 0.21$], 2004 [$P = 0.46$], and 2006 [$P = 0.82$]). Because there was no difference in average growth zone distance for fish collected with either gear type, Taku River Chinook Salmon sampled using fish wheels or set nets were pooled into a single time series (BYs 1979 – 1985, 1990 – 1999, 2002 – 2004), which was used to determine the effect of annual growth on recruitment success. The BYs included in the Unuk River time series were also

collected using multiple gear types (weir, dip net, hook and line, handpicked, and set gill net). Hotellings T^2 tests indicated there were no statistically significant differences between any of the annual growth zones for fish captured using set gill nets and hook and line fishing for age-1.3 (BY 1994 [$P = 0.72$] and 2006 [$P = 0.96$]) or age-1.4 fish (BY 1994 [$P = 0.09$], 2005 [$P = 0.38$], and 2006 [$P = 0.91$]). In addition, no significant differences in mean annual growth were found for weir or handpicked fish (age-1.3 fish from BY 1981, $P = 0.77$) or for fish collected with set gill nets or dip nets (age-1.4 fish from BY 1988, $P = 0.51$). Because annual growth rates were similar for fish collected with each gear type in the Unuk River, fish that were collected using multiple gear types (weir, dip net, hook and line, handpicked, and set gill net) were combined to form a subset of the original time series (BYs 1981 – 1983, 1986 – 1988, 1994 – 2003, 2005 – 2006), which was used in subsequent analyses.

Multiple regression models were constructed separately for each system due to their distinct freshwater and marine rearing locations. Prior to analyzing the data, weighted averages that accounted for differences in the BY abundances of age-1.3 and 1.4 fish were calculated for each annual growth zone and each BY class. The weighted averages for each system were then used to explain the variability in log-transformed BY recruitment benchmarks.

The influence of annual growth on marine survival of stocks from both systems was assessed using weighted simple linear regression. Models were fitted using weighted averages of annual growth zones as explanatory variables and log-transformed marine survival as the response variable. Only annual growth zones that explained high amounts of variation in BY total return and productivity were included in the model due to the fewer number of BYs with marine survival estimates relative to BYs with total return and productivity estimates. The current literature has demonstrated the importance of large body size in determining the survival

and recruitment success of multiple species of Pacific salmon (Mortensen et al. 2000; Beamish et al. 2004; Moss et al. 2005; Farley et al. 2007; Murphy et al. 2013); therefore, statistical significance ($P < 0.05$) of explanatory variables was determined using a one-tailed t-test.

All parameters in the multiple regression and simple linear regression models were estimated using weighted-least-squares regression, with each BY in the model being weighted by the number of scale samples in that BY. Residuals obtained from fitting models were used to test the assumptions of multiple and simple regression analyses (i.e., normality, constant variance, and independence of errors; Quinn and Keough 2002). The assumption of normality was assessed visually by examining normal probability plots for one-to-one relationships between residuals and their theoretical values. The assumption of constant variance was also visually assessed by looking for an even distribution of residuals across the range of fitted values. Because time-series data may lack independence, the presence of temporal autocorrelation was assessed by plotting estimated autocorrelation versus lag distance to determine the magnitude and significance of autocorrelations (Cryer and Chan 2008). Multiple regression models also assumed linear relationships between predictor and response variables. Bivariate scatterplots constructed and examined to determine the nature of the relationships between response and predictor variables. In all models that were fitted, no violations of the previously mentioned assumptions were found. All statistical analyses were performed using R (R Core Team 2014).

Relationship between growth zones

The relationships between adjacent growth zones were examined using mixed-effects modeling. To determine if the growth of individual Chinook Salmon from each system was dependent on their previous growth, random intercept mixed-effects models were fitted by regressing each

individual's annual growth zone on that individual's subsequent annual growth zone (e.g., FW1 versus SW1, SW1 versus SW2, etc.). The relationship between growth zones and BY represented the fixed effect and random effect, respectively. The assumptions of mixed-effects modeling (i.e., normality, constant variance, and independence of errors) were tested using the previously described methods and no violations of these assumptions were found.

Size-selective mortality at ocean entry

The relationship between smolt body size and survival to reproductive maturity was investigated by examining the skew of FW1 by BY freshwater scale growth distributions. Previous research has shown that the length distribution of age-0 Chinook Salmon from the Taku River was normally distributed, and that size-selective mortality of small individuals results in positively skewed weight and length distributions of Chinook Salmon stocks (Murphy et al. 1989; Murphy et al. 2013; Woodson et al. 2013). Because the measured distance of the freshwater growth zone has been used as an index of size at marine entry for both Pacific and Atlantic salmon (Hogan and Friedland 2010; Leon 2013), the freshwater growth distribution was used to represent the length-frequency distribution at ocean entry. Therefore, evidence for size-selective mortality at ocean entry was identified by examining the skew of FW1 distributions by BY. To determine the presence and nature of skew of the FW1 distribution, g_1 was calculated as:

$$g_1 = k_3/s^3,$$

where s^3 and k_3 represent the second and third moments around the mean, respectively (Zar 1999). Positive g_1 values indicated skewed right (positively skewed) distributions and, therefore, g_1 values that were significantly greater than zero implied size-selective mortality during early marine residence. To determine if g_1 values were significantly greater than zero, one-tailed 95%

confidence interval (CI) of BY g_1 values was constructed by bootstrapping the FW1 distributions of each BY class, using 100,000 replicates for each system. The high number of replicates was necessary to produce stable CIs due to BY with large sample sizes.

Previous research indicates that prey abundance and body size may affect predation rates and predator selectivity (Cunningham et al. 2013; Furey et al. 2016). The influence of average smolt length and smolt abundance on g_1 was assessed using simple linear regression analyses. Estimates of BY abundance (Taku and Unuk rivers) and average BY smolt fork length (Unuk River) were obtained from ADF&G. The influence of smolt fork length on g_1 was limited to the Unuk River because smolt fork length data was not collected for the Taku River. The assumptions of simple linear regression (i.e., normality, constant variance, and independence of errors) were tested using the methods outline above and no violations of these assumptions were found.

Results

Brood-year weighted annual growth was highest during the first year at sea, and declined each subsequent year for Chinook Salmon from the Taku and Unuk rivers (Table 1.1). There were no significant trends in the measured distance of any annual growth zone for either system (Table 1.1). Annual growth during freshwater residence displayed significantly lower variability than any other growth zone for Chinook Salmon from the Taku River (1.3-age [ANOVA: $F_{3,88} = 138.6$, $P < 0.001$] and 1.4-age [ANOVA: $F_{4,110} = 75.25$, $P < 0.001$]) and Unuk River (1.3-age [ANOVA: $F_{3,68} = 138.6$, $P < 0.001$] and 1.4-age [ANOVA: $F_{4,85} = 138.6$, $P < 0.001$]).

Relationship between brood year recruitment success and annual growth

For the Taku River, FW1 and SW2 were negatively related to total return, while SW1, SW3, and SW4 were positively related to total return (Figure 1.3). There were no significant relationships between any of the annual growth zones and BY total return or productivity when using sample sizes as weights in the regression model (Figure 1.3; Table 1.2). Overall, annual growth explained little variation in either total return ($R^2_{adj} = 0.07$) or productivity ($R^2_{adj} = 0.07$), when fitting models with weights. However, there appeared to be a positive-linear relationship between total return and first-year marine growth. When both models were fitted without using scale samples sizes as weights and SW1 as the only explanatory variable, first year marine growth explained significant amounts of variation in total return ($R^2 = 0.21$; $P = 0.04$) but not productivity ($R^2 = 0.22$; $P = 0.09$). The 1993 BY had the lowest weight and also had the lowest total return (16,840), productivity (0.21), and weighted first year marine growth (1.08 mm). This BY provided important contrast within the time series and lowering its weight affected the results of the analyses.

In contrast to the Taku River, all annual growth zones were positively related to total return in the Unuk River (Figure 1.3). There was a significant, positive relationship between SW1 and BY total return (Figure 1.3), and no other annual growth zone was significantly related to total return for this stock. Annual growth of Unuk River Chinook Salmon explained more variation in total return ($R^2_{adj} = 0.33$) than did annual growth for the Taku River model ($R^2_{adj} = 0.07$). Similar to the Taku River, no annual growth zones were significant predictors of log-transformed productivity when all of the growth zones were included in the model (Table 1.2). Although there was a strong positive relationship between SW1 and productivity ($P = 0.1$), annual growth explained little variation in productivity ($R^2_{adj} = 0.06$). Because of this

relationship, another model was fitted using only SW1 to explain variance in BY productivity. When SW1 was the only explanatory variable in the model, there was a significant, positive relationship between growth during the first year at sea and stock productivity for Unuk River Chinook Salmon (Table 1.2; $R^2 = 0.26$; $P = 0.03$).

Relationship between annual growth and marine survival

Weighted first-year marine growth was linearly related to marine survival of Taku and Unuk river Chinook Salmon stocks (Figure 1.4). In the Unuk River, there was a significant, positive relationship between marine survival and SW1 (Table 1.3; $R^2 = 0.37$; $P < 0.01$). No other growth zone was significantly related to marine survival for this stock. Similar to the Unuk River, there was a significant positive relationship between marine survival and SW1 of Taku River Chinook Salmon (Table 1.3; $R^2 = 0.32$; $P = 0.04$). There was also a significant positive relationship between SW3 and Taku River Chinook Salmon marine survival (Table 1.3; $R^2 = 0.30$; $P = 0.04$).

Relationship between growth zones

For Unuk River Chinook Salmon, there were no significant relationships between any of the adjacent growth zones (Table 1.4; Figure 1.5). In contrast, there were significant positive relationships between FW1 and SW1 and SW1 and SW2 for Taku River Chinook Salmon (Table 1.4; Figure 1.5). After the second year at sea, there were no significant relationships between any of the remaining adjacent growth zones for Taku River Chinook Salmon (Table 1.4).

Size-selective mortality at ocean entry

In both systems, there was evidence of size-selective mortality at ocean entry. For the Taku River, a total of 33 BY FW1 distributions were examined. Overall, 24 out of the 33 examined BY FW1 distributions had skew values that were greater than zero (Figure 1.6). Further, seven out of thirty-three one tailed 95% CIs were significantly greater than zero. In the Unuk River, 26 BYs FW1 distributions were investigated. Of those 26 BYs, 22 had measured skew values that were greater than zero and 12 of the 26 95% CIs were significantly greater than zero (Figure 1.6).

For Unuk River Chinook Salmon, there was a negative relationship between smolt abundance and the skew of FW1 distribution ($R^2 = 0.25$; $P = 0.07$). Further, there was also a negative relationship between smolt size and the skew of the BY FW1 distribution ($R^2 = 0.27$; $P = 0.06$). For Taku River Chinook Salmon, there was a negative relationship between smolt abundance and skew of the FW1 distribution; however, this relationship was weaker than for the Unuk River ($R^2 = 0.03$; $P = 0.44$).

Discussion

Influence of annual growth on survival

A retrospective scale analysis was conducted using two regionally important salmon-producing systems in an attempt to understand how annual growth influences the survival and recruitment success of Chinook Salmon stocks in SEAK. One important finding of this study was the significant, positive relationship between first-year marine growth and marine survival of Chinook Salmon from the Taku and Unuk rivers. This finding contributes to the considerable

literature indicating the importance of growth and body size during the first marine year in determining marine survival and recruitment success of Pacific salmon (Beamish and Mahnken 2001; Mortensen et al. 2000; Beamish et al. 2004; Moss et al. 2005; Farley et al. 2007; Tomaro et al. 2012; Murphy et al. 2013; Miller et al. 2014). High growth rates during the first year at sea have been associated with greater survival rates of Coho *O. kisutch*, Pink *O. gorbuscha*, Chum *O. keta*, and Chinook Salmon stocks (Healey 1982; Beamish et al. 2004; Farley et al. 2007; Mortensen et al. 2000; Duffy and Beauchamp 2011; Murphy et al. 2013; Woodson et al. 2013; Miller et al. 2014). The positive relationship between growth during early marine residence and survival can be explained by size-selective mortality (Sogard 1997; Beamish and Mahnken 2001). Pacific salmon are thought to experience high rates of size-selective mortality during their first year at sea (Beamish et al. 2004; Farley et al. 2007). Based on the critical size, critical period hypothesis, rapid growth during early marine residence may increase Pacific salmon survival by allowing small individuals to outgrow size classes vulnerable to predation and/or store enough energy to survive the food-limited, first-year marine winter (Sogard 1997; Beamish and Mahnken 2001).

In the current study, the timing of mortality was unknown; therefore, it was not possible to attribute the observed relationship between SW1 and marine survival to reduced size-selective predation during the first few months at sea or to higher survival during the first marine winter. Chinook Salmon stocks within the region are thought to overwinter in the coastal waters of SEAK prior to migrating offshore; therefore, the timing of size-dependent mortality may be determined by sampling Chinook Salmon throughout their first marine year and comparing scale circuli spacing between sampling periods (Beamish et al. 2004; Orsi et al. 2013). Although the timing of mortality was unknown, the results of the current study highlight the importance of

regional conditions that control growth and, ultimately, survival for Chinook Salmon stocks in SEAK. Further, these results suggest that the recent regional declines in Chinook Salmon abundance and productivity may be related to changes in growth conditions during the first year at sea.

Climate plays an important role in shaping the structure and function of aquatic ecosystems, which in turn, may affect the growth rates of Pacific salmon directly through changes in sea-surface temperatures (SSTs) and indirectly through processes that regulate biological production (Benson and Trites 2002; Mueter et al. 2002; Edwards and Richardson 2004; Seo et al. 2006; Noakes and Beamish 2009; Petrosky and Schaller 2010; Hunt et al. 2011; Doney et al. 2012; Shanley and Albert 2014; Wobus et al. 2015). Previous research linked variations in salmon survival with regional SSTs for northern and southern stocks of Pacific salmon (Mueter et al. 2002, 2005). However, the survival of northern and southern species of Pacific salmon was higher during marine entry years characterized by above average and below average SSTs, respectively (Mueter et al. 2002, 2005). The opposite effect of SSTs on survival for northern and southern stocks suggests that SSTs influence the growth and survival of Pacific salmon indirectly through processes that regulate biological production rather than directly through regulation of metabolism (Mueter et al. 2002, 2005). For example, below average SSTs are associated with increased upwelling, primary production, and abundances of lipid-rich copepod species in the California Current Ecosystem, which in turn, are correlated with higher abundances of forage-fish species and increased marine survival of southern stocks of Pacific salmon (Koslow et al. 2002; Peterson and Keister 2003). While recent research suggests that climate variability might influence Pacific salmon survival indirectly through changes in the base of the food web, the mechanisms that indirectly link climate and survival of Pacific salmon are

not well understood (Hertz et al. 2016). Future research should focus on developing a better understanding of how SST variations indirectly influence the growth and survival of Pacific salmon.

Another important finding of the current study was the negligible effect of size at ocean entry (i.e., FW1) on marine survival of Chinook Salmon stocks from both systems. While large smolt body size has been shown to lead to higher survival in Atlantic Salmon and Pacific salmon (Jutila et al. 2006; Woodson et al. 2013), growth during early marine residence appears to have a greater influence on survival than does size at ocean entry in Pacific salmon (Duffy and Beauchamp 2011; Tomaro et al. 2012; Miller et al. 2014). For example, growth during the first 20 days at sea explained more variation in Snake River Chinook Salmon survival than did size at marine entry (Miller et al. 2014). However, large body size may still confer a survival advantage for Pacific salmon smolts, because the probability of experiencing size-selective mortality declines with increases in body size (Murphy et al. 2013). Large-bodied smolts appear to have a survival advantage; however, this advantage appears to be dependent on other factors such as cohort recruitment success and/or growth conditions during early marine residence (Holtby et al. 1990; Woodson et al. 2013; C. Graham, University of Alaska Fairbanks, unpublished data). For example, large smolt body size conferred a survival advantage Chinook and Coho Salmon smolts in years characterized by low, but not high, survival (Holtby et al. 1990; Woodson et al. 2013; Graham, unpublished). Holtby et al. (1990) found that the interannual variations in Coho Salmon survival were driven by early ocean growth rates, which in turn, were strongly correlated with oceanic conditions associated with high biological productivity. This led the authors to speculate that the relationship between smolt body size and survival may be dependent on early ocean growth conditions. Because the relationship between smolt body size and survival may depend

on cohort survival and/or growth conditions during early marine residence, future research should focus on of how these factors interact to better understand the relative importance of growth in freshwater versus marine residence in determining the marine survival of Chinook Salmon within SEAK.

Size-selective mortality is the proposed mechanism that explains the positive relationship between growth and survival; therefore, the majority of current research examining the factors that influence Pacific salmon survival has focused on processes that occur when salmon inhabit size classes that are thought to be most susceptible to size-based predation (i.e., freshwater residence, early marine residence; Sogard 1997; Beamish and Mahnken 2001; Murphy et al. 2013; Woodson et al. 2013; Miller et al. 2014). However, because Chinook Salmon stocks may spend upwards of seven years in the marine environment, causes of mortality that occur after early ocean residence must be considered when examining the mortality dynamics of this species. Greene et al. (2005) examined the relationship between Skagit River Chinook Salmon return rates and environmental conditions during freshwater, estuarine, and marine residence and found a significant relationship between a factor negatively related to SSTs and positively related to sea level pressure and coastal upwelling during the third marine year and stock productivity. The authors postulated that conditions during the third year at sea could influence the energetic efficiency of spawning migrations with poor conditions (i.e., high SSTs) leading to increased energy expenditures and reduced survival. In the current study, enhanced growth during the third year at sea was associated with higher marine survival of Chinook Salmon from the Taku River. This stock of Chinook Salmon is thought to rear in the Gulf of Alaska and Bering Sea where they may be selectively targeted by predators such as Killer Whales *Orcinus orca* and/or Salmon Sharks *Lamna ditropis* (Ford et al. 1998; Nagasawa 1998; Ford and Ellis 2006). Because of the

positive relationship between body size and swimming ability, high growth during the third year at sea may increase survival by allowing Chinook Salmon to escape potential predators. Current research using satellite pop-up-satellite tags suggests that Chinook Salmon with a mean fork length of 69 cm (range, 57 – 89 cm) in the Bering Sea and Gulf of Alaska may experience predation by both homeothermic and poikilothermic predators (M. Courtney, University of Alaska Fairbanks, personal communication). Therefore, size-selective mortality may explain the observed relationship between growth during the third year at sea and marine survival of Taku River Chinook Salmon.

Growth dependency

Results of the current study indicate that annual growth of individual Chinook Salmon from the Taku River is dependent on their previous annual growth through the second year at sea. Growth dependency between adjacent growth zones has also been found in individual Chinook Salmon from the Yukon and Kuskokwim rivers (Ruggerone et al. 2009; Leon 2013). As noted by Ruggerone et al. (2009), growth dependency may be the result of developmental changes in prey availability and the highly piscivorous diet of Chinook Salmon (Quinn 2005; Davis et al. 2009). In general, as Chinook Salmon increase in size, their diets contain higher proportions of fish (Schabetsberger et al. 2003). High growth rates during freshwater residence could allow an earlier transition to fish-based diets, which in turn, could increase growth rates during the first year at sea due to their higher energy content (Boldt and Haldorson 2002; Pazzia et al. 2002).

In the current study, growth dependency between adjacent growth zones was present through the second year at sea. However, growth in Chinook Salmon from the Yukon and Kuskokwim rivers was dependent on previous growth for each set of adjacent annual growth

zones (Ruggerone et al. 2009). One possible reason for the difference in results between the current study and Ruggerone et al. (2009) was that the latter study used the five widest adjacent circuli in the previous growth zone as explanatory variables, while the current study used the entire distance of the previous annual zone. The diets of Chinook Salmon can be influenced by local prey availability (Weitkamp and Sturdevant 2008; Myers et al. 2009); therefore, the greater growth dependency of Yukon and Kuskokwim river Chinook Salmon relative to Taku River Chinook Salmon may be the result of different marine rearing locations. However, opportunistic recoveries of coded-wire tags indicate that the marine distributions of these stocks may overlap in the Bering Sea (Bugaev and Myers 2009; McPherson et al. 2010).

Size-selective mortality at ocean entry

The results of the current study indicate that Chinook Salmon from the Taku and Unuk rivers may experience size-selective mortality at ocean entry. Pacific salmon smolts are thought to face high rates of size-selective predation when entering predator-rich coastal environments (Quinn 2005; Murphy et al. 2013). Murphy et al. (2013) compared the weight distributions of juvenile and mature Chinook Salmon from the Yukon River and found that heavier smolts were more likely to survive their ocean residence than lighter individuals within the cohort. Due to the strong positive relationship between length and weight in Chinook Salmon smolts (Tattam et al. 2015), the results from Murphy et al. (2013) implied that longer fish also had higher survival. In addition, Woodson et al. (2013) found that large-bodied Chinook Salmon smolts from California's Central Valley were more likely to survive the first month at sea than smaller members of their cohort. In the current study, FW1 distributions of stocks from both systems were positively skewed more than would be expected by chance, with 21% of the Taku River

Chinook Salmon and 46% of the Unuk River Chinook Salmon BY FW1 distributions exhibiting significant, positive skew. The higher percentage of significantly skewed FW1 distributions for Unuk River Chinook Salmon may be attributed to their relatively lower smolt abundance than Taku River Chinook Salmon. High abundances have been shown to reduce the per-capita predation rates of Sockeye Salmon *O. nerka* (Furey et al. 2016). However, few studies have investigated how prey abundance affects the size selectivity of predators. Cunningham et al. (2013) found that in years of high Sockeye Salmon abundances, Brown Bears *Ursus arctos* exhibited lower rates of size selectivity. In the current study, smolt abundance and skew of the freshwater growth distributions were negatively related for both systems, which implied lower levels of size-selective mortality when Chinook Salmon abundances were high. Therefore, if high smolt abundances reduce the rate of size-selective mortality, then freshwater growth may be more important for reducing size-selective mortality at ocean entry for smaller stocks within the region.

One limitation of the use of the skewness of FW1 distributions to identify size-selective mortality at ocean entry was the unknown length distribution of outmigrating smolts. If Pacific salmon face high rates of size-selective mortality during freshwater residence, their length distributions may become positively skewed prior to ocean entry. In addition, large fish may become dominant and, as a result, become better able to compete for resources (Abbott and Dill 1989); consequently, the observed skew in freshwater growth distributions may also be the result of larger fish growing at faster rates than smaller individuals within these stocks. Previous research indicates that freshwater length distribution of age-0 Chinook Salmon from the Taku River was is normally distributed (Murphy et al. 1989). The results of the current study (i.e., negative relationship between both smolt abundance and size and skew of the FW1 distribution)

in conjunction with previous research, which found evidence of size-selective mortality at ocean entry, suggest that the observed skew of FW1 distributions from both systems is the result of size-selective mortality during early marine residence. In addition, the variability of the in BY FW1 distributions was significantly lower than any other annual growth zone for Chinook Salmon from both systems, suggesting selection for a minimum smolt body size to survive to reproductive maturity. Future research that compares the freshwater growth increment of smolts sampled during or shortly after their outmigration with mature fish sampled during their spawning migration could provide more convincing evidence of size-selective mortality at ocean entry (Murphy et al. 2013).

While freshwater growth explained negligible amounts of variation in the marine survival and recruitment success of Chinook Salmon stocks from both systems, it may influence survival patterns by reducing size-selective predation during early marine residence and enhancing early marine growth of Chinook Salmon. Anticipated changes of freshwater systems in SEAK due to climate change could impact the freshwater growth of stocks from both systems. In SEAK, average winter air temperatures (^{o}C) are near freezing; therefore, small increases in water temperature could have profound effects on the structure and function of freshwater systems within the region (Shanley and Albert 2014). For example, model simulations suggest that small increases in air temperature will alter precipitation patterns and lead to an overall increase in freshwater discharge in SEAK (Shanley and Albert 2014). Increased winter water temperatures may increase basal metabolic rates and, without concurrent increases in food availability, lead to decreased growth rates (Groot et al. 1995). Further, lower summer water temperatures from increased glacial melting could reduce metabolic rates and, consequently, growth in salmon. Future research should focus on developing a better understanding of how anticipated changes of

freshwater ecosystems due to climate change will affect the growth and, potentially, survival of stocks within the region.

The results of the current study highlight the importance of growth during the first marine year in influencing the survival of Pacific salmon stocks in SEAK and suggest that the current declines in Chinook Salmon abundance within the region may be attributed to changes in growth or growth conditions during the first year at sea. While growth during freshwater residence was not related to the survival or recruitment success of either stock, it may still influence Chinook Salmon survival patterns by facilitating early ocean growth rates and reducing size-selective mortality at ocean entry. Finally, while the majority of the current research has focused on processes during freshwater and early marine residence when trying to describe variability in recruitment success and survival, results of this study indicate that survival may be influenced by processes happening later in the life of Chinook Salmon (i.e., third year of marine growth).

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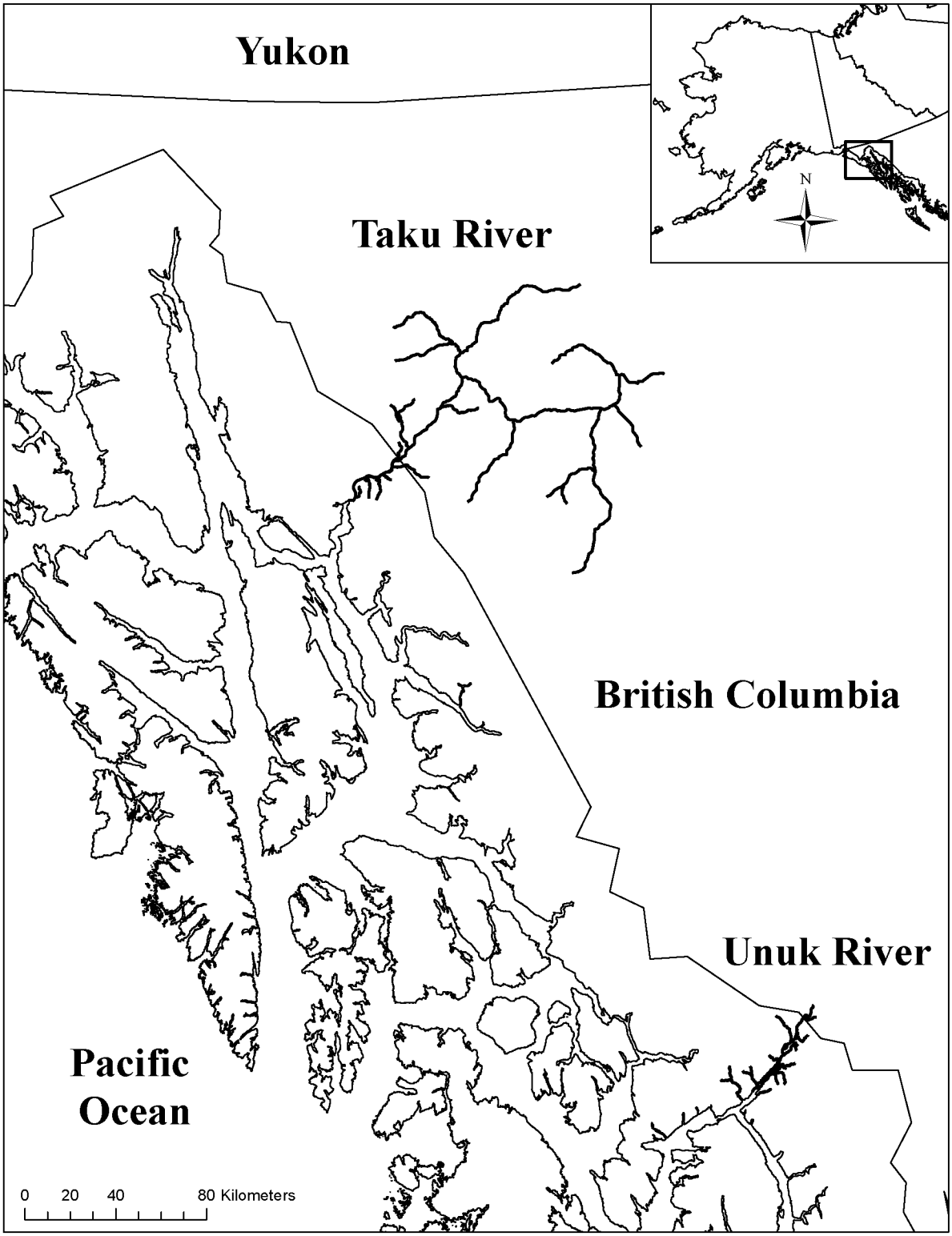

Figure 1.1. Location of the Taku and Unuk rivers in Southeast Alaska and British Columbia.

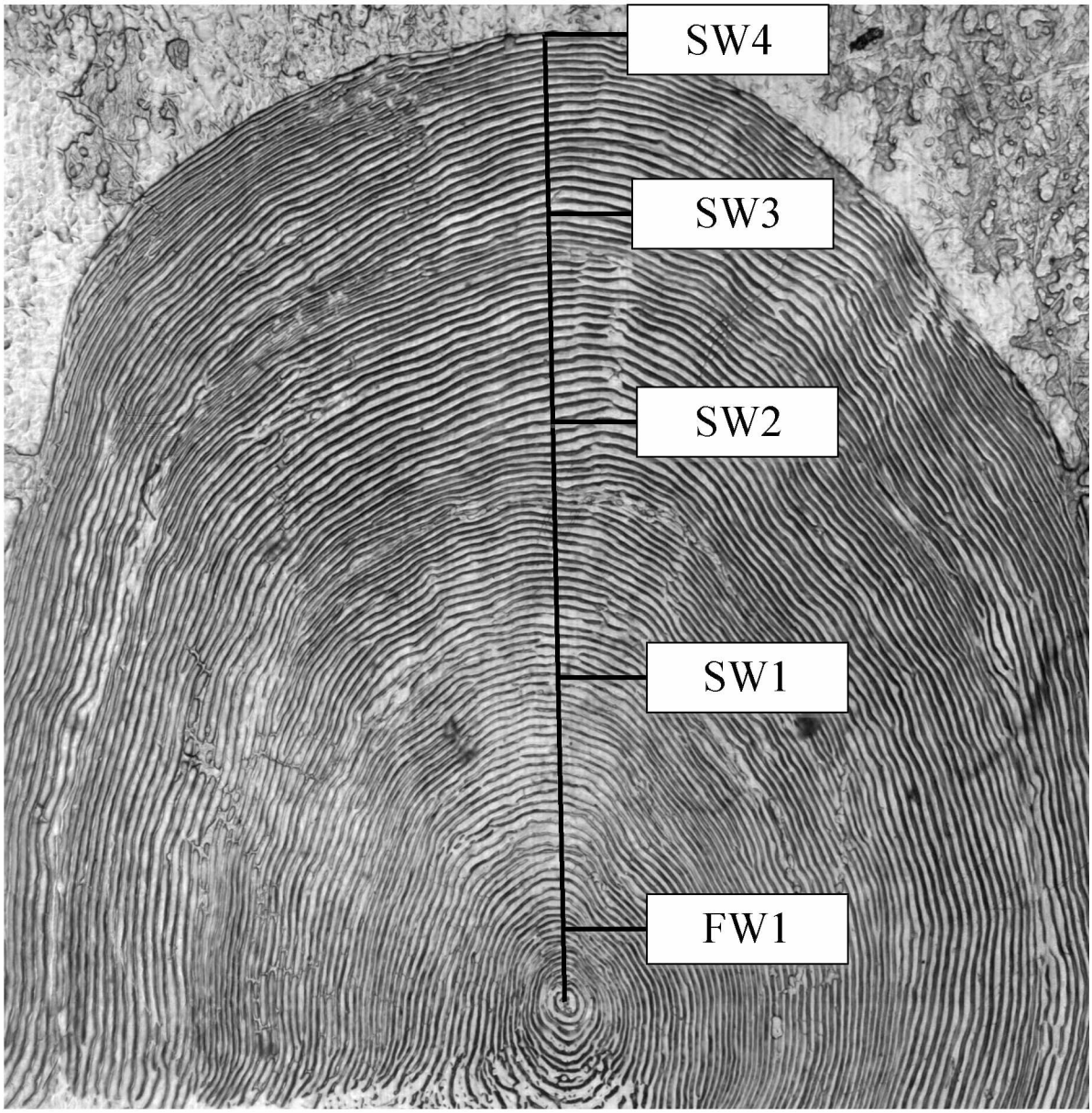

Figure 1.2. Age-1.4 Chinook Salmon scale from the Taku River displaying growth in freshwater (FW1) and the first (SW1), second (SW2), third (SW3) and fourth (SW4) years of marine growth.

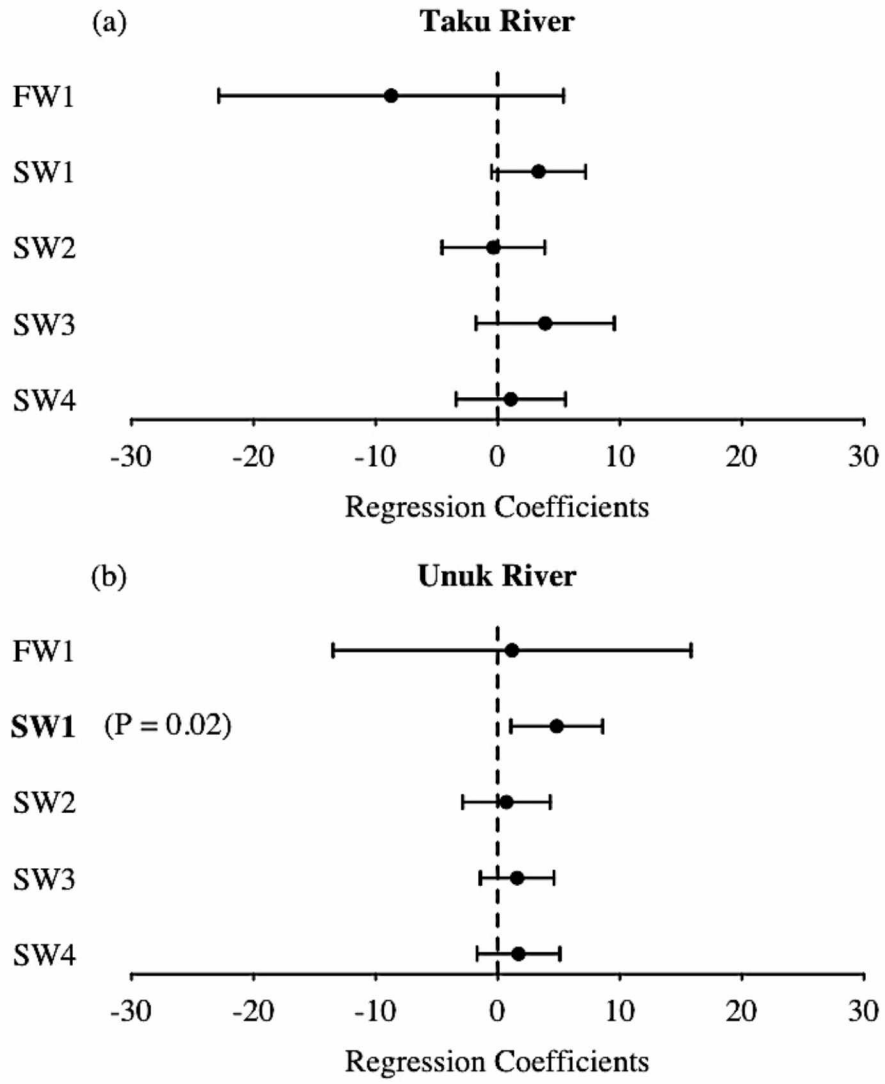

Figure 1.3. Visualization of the multiple regression models that were fitted using weighted annual growth zones (freshwater growth [FW1], first [SW1], second [SW2], third [SW3], and fourth [SW4] years of marine growth) on the y axis to explain variance in brood-year total return in the (a) Taku and (b) Unuk rivers. On the x axis are the estimated regression coefficients and their 95% CIs. The dashed vertical line is at zero; coefficients that fall to the right and left of the line indicate a positive and negative relationship between that annual growth zone and brood-year total return, respectively. Weighted annual growth zones in bold were found to explain statistically significant ($P < 0.05$) amounts of variance in brood-year total return.

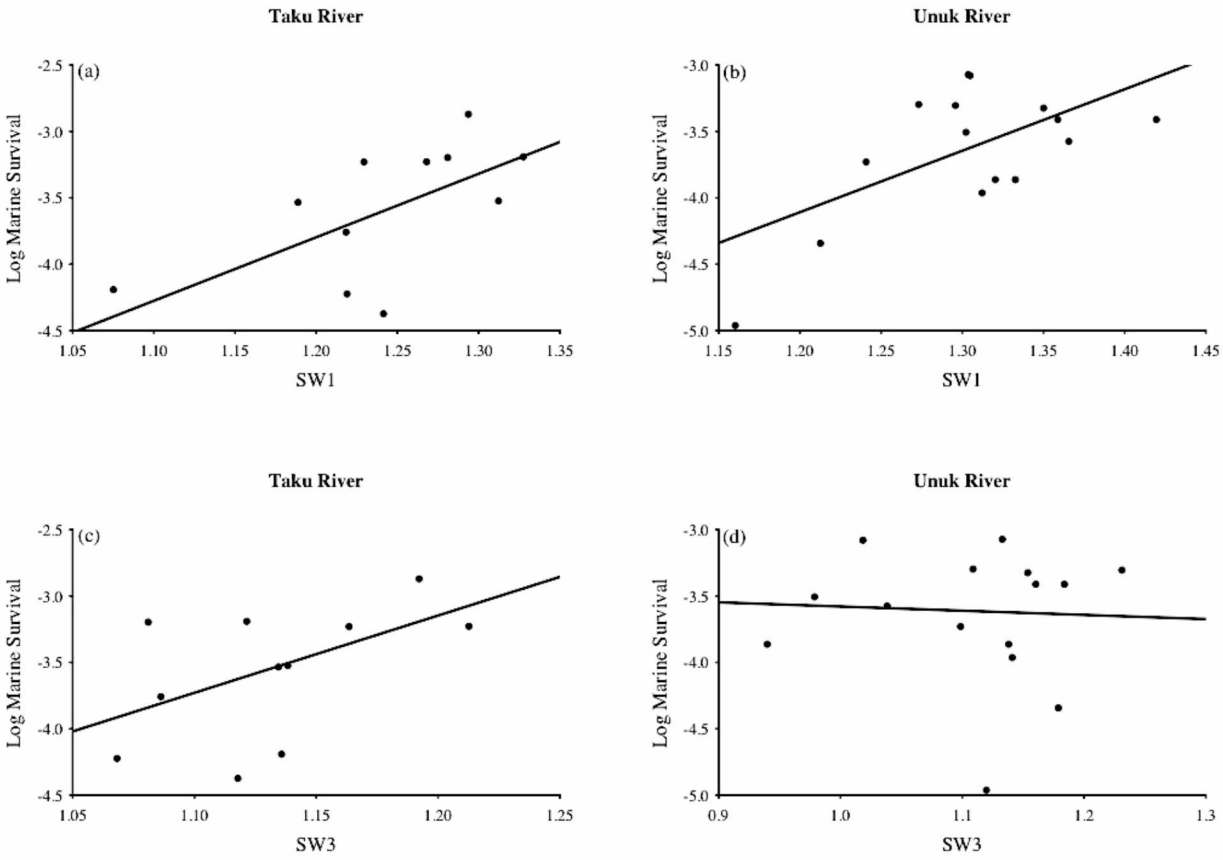

Figure 1.4. Scatter plots showing relationships between first- and third-year marine growth and marine survival for (a, c) Taku and (b, d) Unuk river Chinook Salmon. The solid black line was obtained from simple linear regression models that used annual growth to explain variance in marine survival.

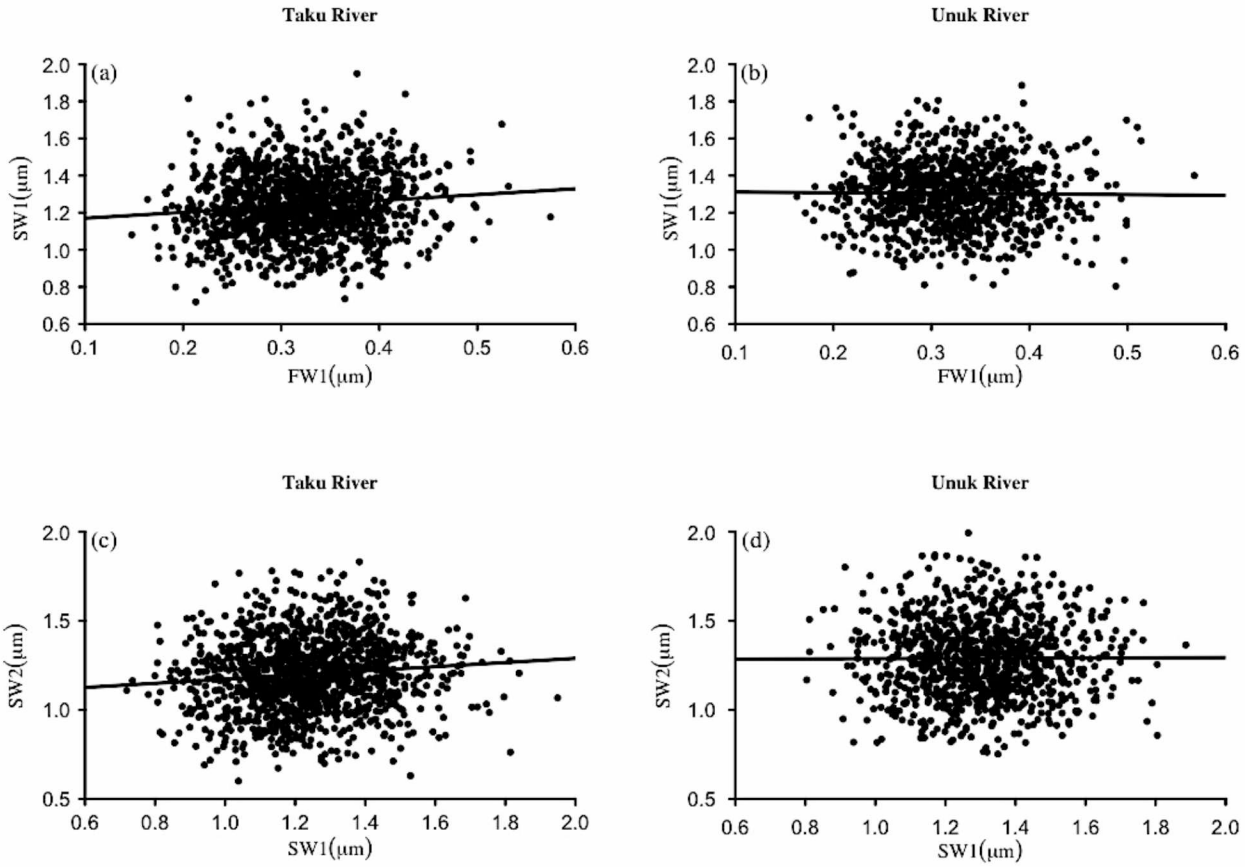

Figure 1.5. Relationships between adjacent growth zones in (a, c) Taku and (b, d) Unuk river Chinook Salmon stocks. The lines were obtained by fitting simple linear regression models using the previous growth zone to predict the subsequent growth zone.

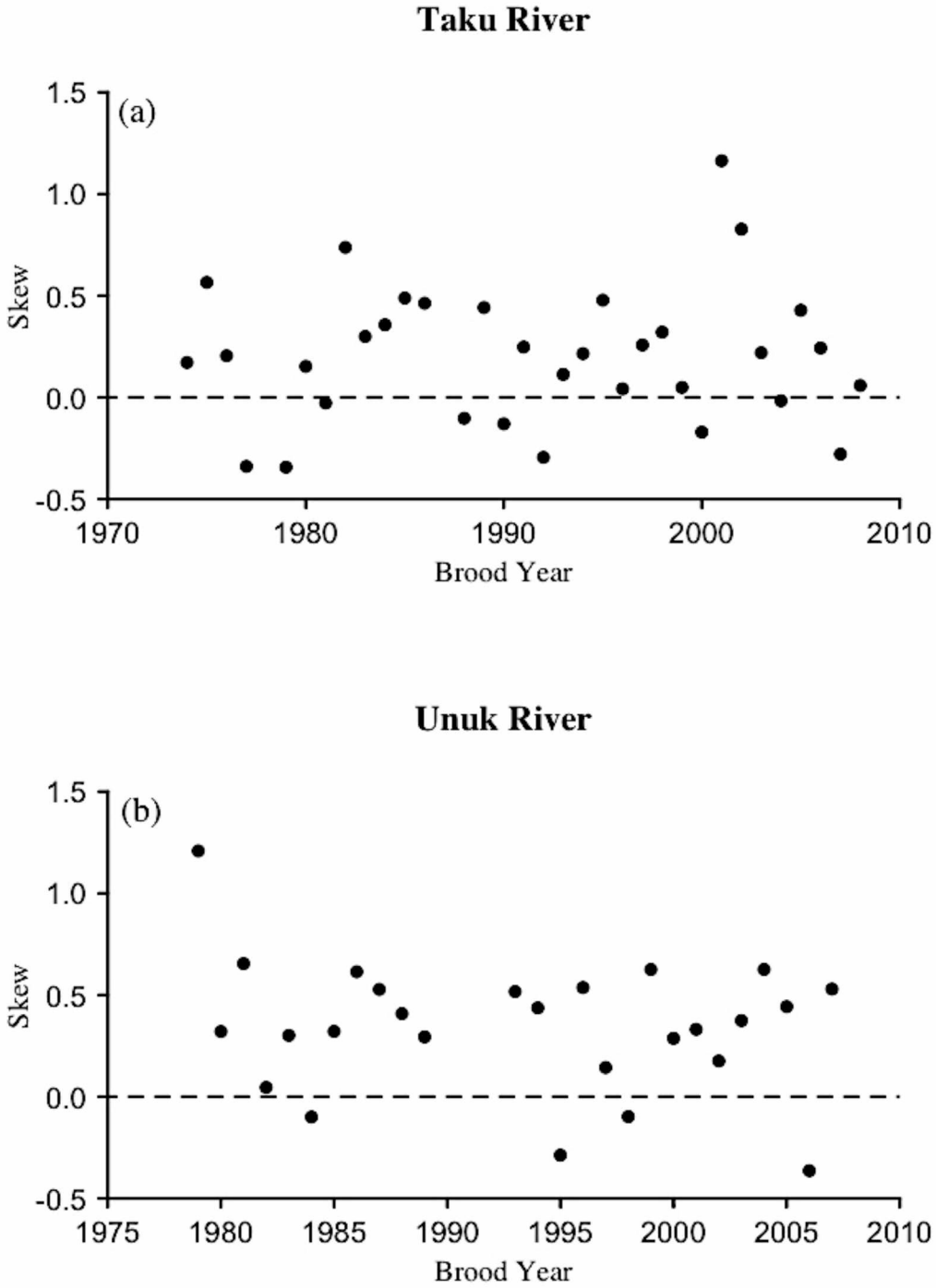

Figure 1.6. Scatter plot with skew of brood-year freshwater growth distributions on the y axis and brood year on the x axis for the (a) Taku and (b) Unuk rivers. The dashed line is at zero; points that fall above the line indicate positive skew of freshwater growth distribution.

Table 1.1. Mean distance, range, and standard deviation of weighted annual growth zones (freshwater growth [FW1], first [SW1], second [SW2], third [SW3], and fourth [SW4] years of marine growth), by brood year, for Taku and Unuk river Chinook Salmon stocks. Regression coefficients (β), standard errors, t-values, and *P*-values were obtained from simple linear regression models that regressed each annual growth zone on brood year to determine if there were trends in annual growth across the time series.

System	Growth zone	Mean growth	Range	SD	β	Standard error	t-value	*P*-value
Taku River	FW1	0.32	0.28 – 0.35	0.02	< -0.001	< 0.001	-0.47	0.64
	SW1	1.25	1.08 – 1.35	0.07	< -0.001	0.002	-0.36	0.72
	SW2	1.21	1.09 – 1.31	0.07	0.001	0.002	0.88	0.39
	SW3	1.11	0.99 – 1.21	0.05	< -0.001	0.001	-0.14	0.89
	SW4	0.79	0.69 – 0.96	0.06	-0.002	0.001	-1.46	0.16
Unuk River	FW1	0.32	0.29 – 0.36	0.02	< -0.001	0.001	-1.82	0.09
	SW1	1.30	1.16 – 1.41	0.07	-0.002	0.002	-0.98	0.34
	SW2	1.29	1.15 – 1.43	0.08	0.002	0.002	0.92	0.37
	SW3	1.11	0.94 – 1.23	0.08	-0.004	0.002	-1.48	0.16
	SW4	0.76	0.69 – 0.92	0.07	-0.003	0.002	-1.79	0.09

Table 1.2. Results of weighted multiple regression models (regression coefficient [β]) that examined the influence of weighted annual growth (freshwater growth [FW1], first [SW1], second [SW2], third [SW3], and fourth [SW4] years of marine growth) on log-transformed brood-year productivity for Taku and Unuk river Chinook Salmon.

		Model				
Dependent variable	Independent variable	β	Standard error	t-value	*P*-value	Adjusted R-squared
Taku River						
Productivity	FW1	2.97	9.96	0.30	0.77	0.07
	SW1	3.05	2.72	1.12	0.28	
	SW2	-5.09	2.97	-1.71	0.11	
	SW3	3.12	4.00	0.78	0.45	
	SW4	-0.26	3.16	-0.08	0.94	
Unuk River						
Productivity	FW1	5.51	11.63	0.47	0.64	0.06
	SW1	5.31	2.98	1.78	0.10	
	SW2	1.24	2.84	0.44	0.67	
	SW3	1.32	2.39	0.55	0.59	
	SW4	1.56	2.69	0.58	0.57	
Productivity	SW1	5.14	2.12	2.43	0.03	0.22

Table 1.3. Results of weighted simple linear regressions (regression coefficient [β]) that examined the influence of weighted annual growth during the first (SW1) and third (SW3) years at sea on the marine survival of Taku and Unuk river Chinook Salmon.

		Model				
Dependent variable	Independent variable	β	Standard error	t-value	*P*-value	R-squared
Taku River						
Marine survival	SW1	4.79	2.35	2.04	0.04	0.32
	SW3	5.82	2.99	1.94	0.04	0.30
Unuk River						
Marine survival	SW1	4.63	1.69	2.74	< 0.01	0.37

Table 1.4. Pearson's product-moment correlation coefficient (r) and results of mixed-effects models (regression coefficient [β], and degrees of freedom [DF]) that examined the relationships between adjacent growth zones (freshwater growth zone [FW1], and first [SW1], second [SW2], third [SW3], and fourth [SW4] year marine growth zones) of individual fish collected in the Taku and Unuk rivers.

			Model				
Dependent variable	Independent variable	r	β	Standard error	DF	t-value	*P*-value
Taku River							
SW1	FW1	0.11	0.32	0.078	1273	4.040	< 0.001
SW2	SW1	0.10	0.12	0.031	1273	3.916	< 0.001
SW3	SW2	-0.03	-0.02	0.027	1178	-0.677	0.50
SW4	SW3	-0.08	-0.04	0.036	481	-1.089	0.28
Unuk River							
SW1	FW1	-0.01	0.08	0.089	966	0.948	0.34
SW2	SW1	0.01	-0.04	0.040	965	-1.008	0.31
SW3	SW2	-0.07	-0.03	0.033	739	-0.873	0.38
SW4	SW3	0.05	0.04	0.057	211	0.781	0.44

Chapter 2: Influence of abiotic and biotic factors on the freshwater overwinter survival of Unuk River Chinook Salmon[1]

Abstract

Variability in the freshwater survival rates of Chinook Salmon *Oncorhynchus tshawytscha* may influence brood-year (BY) recruitment strength. However, the relative influence of biotic and abiotic factors in determining freshwater survival and smolt production of Chinook Salmon is unknown. Principal component analysis was used in conjunction with principal component regression to determine the influence of parr body size (i.e., length [mm] and weight [g]), stream discharge (m^3/s), and air temperature (^oC) on freshwater overwinter survival (BY 1993, 1995 – 2007) and smolt production (BY 1993, 1995 – 2008) of Chinook Salmon in the Unuk River (Southeast Alaska). Neither biotic nor abiotic factors were significantly related to freshwater overwinter survival or smolt production. However, a principal component that loaded on spring air temperature and spring and fall discharge explained the most variation in smolt production ($R^2 = 0.23$; $P = 0.07$), indicating that cool spring temperatures and low spring and fall discharge were associated with high smolt production of Chinook Salmon in the Unuk River. These results suggest that anticipated changes in freshwater systems in Southeast Alaska due to climate change may result in lower smolt production in the region.

[1] Graham, C. J., T. M. Sutton, M. V. McPhee, M. D. Adkison, and P. J. Richards. 2016. Influence of abiotic and biotic factors on the freshwater overwinter survival of Unuk River Chinook Salmon. Prepared for submission to Transactions of the American Fisheries Society.

Introduction

Chinook Salmon *Oncorhynchus tshawytscha* are harvested in commercial, sport, and subsistence fisheries in Southeast Alaska (SEAK) due to their value as social, cultural, and economic resources (Der Hovanisian et al. 2011). However, recent declines in abundance and spawning run sizes of Chinook Salmon within the region have resulted in management restrictions and, consequently, reductions in sport and commercial landings. For example, there has been an 8% decline in sport fish landings and a 4% decline in commercial harvests in SEAK from 1994 – 2006 to 2007 – 2011, respectively (ADF&G Chinook Salmon Research Team 2013). Because of the high value of this species, harvest restrictions and reduced landings may cause social and economic hardships for multiple user groups within the region; therefore, it is important to understand the factors contributing to the current declines in the abundance and survival of Chinook Salmon in SEAK.

Pacific salmon brood-year strength is thought to be determined by biotic and abiotic factors during freshwater and early marine residence (Mortensen et al. 2000; Beamish and Mahnken 2001; Koslow et al. 2002; Mueter et al. 2002; Quinn 2005; Hurst 2007; Brown et al. 2011; Miller et al. 2014). However, few studies have examined how these factors influence the survival of Pacific salmon during the freshwater overwinter period. Because the impact of biotic and abiotic factors on freshwater overwinter survival of Pacific salmon may be large enough to influence brood-year recruitment success (Bradford 1995; Hurst 2007; Brown et al. 2011), this lack of research has contributed to a critical knowledge gap that must be addressed to understand current declines in the abundance of Chinook Salmon stocks in SEAK.

The survival of Pacific salmon during the freshwater overwinter period may be mediated by size-selective processes (Quinn and Peterson 1996; Meyer and Griffith 1997; Biro et al. 2004; Hurst 2007; Brown et al. 2011). Predation is thought to be an important cause of mortality for salmonids while they overwinter in freshwater systems, with juveniles being exposed to a suite of potential aquatic and terrestrial predators (Peterson 1982; Quinn 2005; Hurst 2007; Brown et al. 2011). Large body size may reduce the risk of predation in two ways (Sogard 1997). First, large body size may physically prevent predation due to mechanical feeding restrictions (i.e., gape size limitations) in predators (Sogard 1997; Juanes et al. 2002; Dörner and Wagner 2003). Second, there is a positive relationship between body size and swimming ability; therefore, large-bodied fish may be better able to escape potential predators than small-bodied members of their cohort (Juanes 1994). Large body size may also reduce the risk of starvation-induced mortality during the freshwater overwinter period (Biro et al. 2004; Hurst 2007; Brown et al. 2011). This period is physiologically stressful and associated with reductions in body condition and energy reserves of salmonids (Cunjak 1988; Steinhart and Wurtsbaugh 2003; Huusko et al. 2007; Hurst 2007; Brown et al. 2011). Positive relationships between body size and overwinter survival have been identified for Rainbow Trout *O. mykiss*, Atlantic Salmon *Salmo salar*, and Coho Salmon *O. kisutch*, with this relationship being attributed to the higher energy reserves and metabolic efficiency of large relative to small fish (Smith and Griffith 1994; Schultz and Conover 1999; Biro et al. 2004; Hurst 2007; Brown et al. 2011). Because of the importance of size-selective processes in determining the overwinter survival of salmonids, variations in parr body size may influence the survival of Pacific salmon during the freshwater overwinter period.

In addition to body size, stream discharge may affect freshwater survival, due to its influence on habitat availability and foraging efficiency of drift-feeding salmonids (Gibson and

Myers 1988; Cunjak et al. 1998; Lobón-Cerviá and Rincón 2004; Neuswanger et al. 2015). Low stream discharge may reduce habitat availability and, consequently, survival during the overwinter period. For example, Cunjak et al. (1998) found a positive relationship between winter discharge and interannual survival of juvenile Atlantic Salmon. In contrast, high fall and spring discharge may increase turbidity and debris load, which in turn, may reduce the foraging efficiency and survival of drift-feeding salmonids (Neuswanger et al. 2015). Therefore, stream discharge may influence the survival of salmonids during freshwater residence with its effect depending on season.

Water temperature may also influence overwinter survival of stream-dwelling salmonids due to its regulation of metabolic rates (Lawson et al. 2004; Huusko et al. 2007). Because metabolic rates of poikilotherms are positively related to temperature, low winter water temperatures may lead to reduced survival of Pacific salmon during the freshwater overwinter period. Low water temperatures may compromise the swimming ability of salmonids, which in turn, may decrease survival through increased susceptibility to endothermic predators and decreased ability to respond to changes in the environment (Hurst 2007; Brown et al. 2011). In addition, low water temperatures may decrease salmonids ability to capture and assimilate prey resources, which could lead to energy deficits, depleted energy reserves and starvation-induced mortality (Cunjak et al. 1987, 1988; Huusko et al. 2007; Hurst 2007; Brown et al. 2011). Because of the importance of water temperature in influencing the overwinter survival rates of salmonids, anticipated changes in water temperatures of freshwater systems due to climate change may alter survival patterns of Chinook Salmon in SEAK.

Climate change may alter freshwater systems that Chinook Salmon inhabit in SEAK, which in turn, may lead to changes in survival. In this region, average winter air temperatures are

near freezing (-4°C; Simpson et al. 2005); therefore, small increases in air temperature could have large effects on the flow regimes of freshwater systems within the region (Shanley and Albert 2014). For example, model simulations suggest that higher regional air temperatures (~3°C) will alter precipitation patterns and lead to an overall increase in freshwater discharge in SEAK (Shanley and Albert 2014). In addition, higher air temperatures may result in warmer winter water temperatures, which could lead to increased basal metabolic costs and reduced survival if food is limited during the overwinter period (Elliott 1988; Hurst 2007; Brown et al. 2011). Therefore, it is important to evaluate the influence of abiotic factors on the overwinter survival of salmonids in SEAK to anticipate how future changes in freshwater systems may affect the overwinter survival of Chinook Salmon.

Whereas biotic and abiotic factors are known to influence the survival of salmonids in freshwater systems, their relative influence on overwinter survival and smolt production of Chinook Salmon stocks in SEAK is unknown. In this study, principal component analysis (PCA) was used in conjunction with principal component regression (PCR) to examine the influence of fall (October – November) and spring (March – April) abiotic (water temperature and river discharge) and biotic (parr length [mm] and weight [g]) factors on the freshwater overwinter survival and smolt production of an important Chinook Salmon producer in SEAK (i.e., Unuk River). The results of this study will contribute to the knowledge of the influences of the freshwater survival of a regionally important Chinook Salmon stock.

Methods

Study site

The Unuk River is a glacially influenced, transboundary system that originates in British Columbia, Canada, and empties into Behm Canal approximately 85 km east of Ketchikan, SEAK (Figure 2.1; Hendrich et al. 2008). The system was chosen for this study for multiple reasons. First, the Unuk River is, on average, the fourth-largest producer of Chinook Salmon within SEAK, with annual runs of approximately 5,500 large fish (> 660 mm) per year (Der Hovanisian et al. 2011). In addition, a proposed, large-scale mining development threatens pristine spawning and rearing habitats of Chinook Salmon on the Unuk River (Pahlke et al. 1995; Canadian Environmental Assessment Agency 2014). For example, the Kerr-Sulphurets-Mitchell mine (KSM) is a proposed transboundary, open-pit mine located on Sulphurets Creek in northern British Columbia, which is a tributary of the Unuk River. As planned, KSM will be similar in scale to the proposed Pebble Mine. Due to its large size, over 450,464 L of contaminated water per minute will be treated prior to storage in a 165 m tall earthen dam (Canadian Environmental Assessment Agency 2014). The location of the proposed KSM dam and the long-term storage of waste threatens pristine spawning and rearing habitat for Chinook Salmon and other Pacific salmon stocks. It is estimated that approximately 83% of Chinook Salmon from the Unuk River spawn downstream from the Canadian border (Pahlke et al. 1995). Therefore, large segments of Unuk River Chinook Salmon are susceptible to the proposed mine development.

Biological data

Results from the Alaska Department of Fish and Game (ADF&G) Unuk River coded-wire tag (CWT; 1992 – present) and mark-recapture program (1997 – present) allowed the estimation of parr biological attributes (i.e., fork length [mm] and weight [g]), freshwater overwinter survival (brood years [BY] 1993–2007), and smolt production of Unuk River Chinook Salmon (BY 1993 – 2008; Hendrich et al. 2008; Weller and Evans 2012). Data from subsequent BYs (i.e., 2009 – present) were not included in these analyses because all Chinook Salmon from these BYs have yet to return from the ocean; therefore the ADF&G has not yet estimated their freshwater overwinter survival.

Parr and smolt capture, tagging, and sampling

Chinook Salmon parr and smolts were captured by the ADF&G using minnow traps (420 mm long × 191 mm diameter, with 6-mm mesh) baited with salmon roe in back eddies and major sloughs of the lower portion of the Unuk River each fall (October) and spring (March – May; Hendrich et al. 2008; Weller and Evans 2012). All captured fish ≥ 50 mm fork length (FL) that were not missing an adipose fin were implanted with a coded-wire tag (CWT), unique to their season, and marked by removing their adipose fin to facilitate future identification. Annual systematic subsamples of 188 par were measured to the nearest 1 mm and weighed to the nearest 1 g to estimate mean length and weight with 95% relative precision.

Smolt abundance and freshwater overwinter survival

The BY abundance of Unuk River Chinook Salmon smolts was estimated by the ADF&G using a two-event mark-recapture experiment using a modified Chapman-Petersen formula (Seber

1982; Weller and Evans 2012). In the first event, smolts were implanted with CWTs and marked as previously described. In the second event, adults were sampled on the spawning grounds when estimating the in-river abundance of mature Chinook Salmon. Because previous studies conducted by the ADF&G have shown that the proportion of adults from a BY with CWTs did not vary considerably over return years (Weller and Evans 2012), the number of adults with spring CWTs were used to estimate the ratio of marked and unmarked fish in the second event. Then, the ADF&G estimated parr abundance using the number of adults with fall coded-wire tags in the same manner. Freshwater overwinter survival was estimated as the ratio of smolt to parr abundance.

Physical data

Mean monthly stream discharge (m^3/s) data for the Stikine River (1976 – 2014) near Wrangell, Alaska (USGS gauging station #15024800), was received from the United States Geological Survey (USGS; http://www.usgs.gov/). While it would have been preferable to use local discharge data from the Unuk River for these analyses, indexed discharge data for this system over the time period of the study did not exist. Discharge data for the Unuk River near Stewart, British Columbia (USGS gauging station #15015590), was available from July 1960 to March 1996. Based on the overlapping discharge data for the Stikine and Unuk rivers, simple linear regression indicated that there was a significant, positive relationship ($P = < 0.001$, $r = 0.96$) between discharges of the two systems; therefore, stream discharge data from the Stikine River was used in the subsequent analyses. From Stikine River monthly mean discharge data, spring (March – April) and fall (October – November) discharge averages were calculated and used in the subsequent analyses. These specific months were chosen for the fall and spring discharge

indices because the Unuk River is usually ice covered from December – February (T. Johnson, ADF&G, personal communication) and transitional periods between seasons have been associated with high acclimation costs which may lead to mortality (Cunjak 1988; Biro et al. 2004).

Water temperature data were not available for the Unuk River over the time period used in this study. Instead, air temperature was used as a proxy for water temperature when modeling overwintering survival and smolt production of Unuk River Chinook Salmon. Air and water temperature tend to be correlated at moderate, non-freezing temperatures (i.e., between 0-20^{o}C; Mohseni and Stefan 1999). For instance, Lawson et al. (2004) used ambient air temperature as a proxy for water temperature and found evidence for a negative relationship between air temperature and freshwater survival of Coho Salmon. Average monthly air temperature data were received from the National Weather Service (http://www.ncdc.noaa.gov/) for the Ketchikan Airport due to its close proximity to the Unuk River (closest weather station; approximately 90 km from the mouth of the Unuk River) and because air temperature was collected consistently over the study period (1992 – 2007). Because air and water temperatures are only correlated at moderate values (Mohseni and Stefan 1999; Fellman et al. 2014), and the Unuk River is ice free from March until the end of November (T. Johnson, ADFG, personal communication), fall and spring temperature indices were created by averaging October – November and March – April air temperatures, respectively.

Data analyses

To determine the influence of biotic and abiotic factors on the freshwater overwinter survival and smolt production of Chinook Salmon, PCA was used in conjunction with PCR (Quinn and

Keough 2002). Principal component analysis was the appropriate statistical technique to analyze this dataset due to the low number of observations (14 BYs) relative to the number of explanatory variables (six) and because the examined biotic and abiotic variables exhibited multicollinearity. Biotic (i.e., mean parr length [mm] and weight [g]) and abiotic variables (i.e., mean fall and spring temperature [^{o}C] and discharge [m^3/s]) were entered into a correlation matrix and their dimensions were reduced using PCA. Abiotic variables were lagged (fall [BY + 1], spring [BY + 2]) to represent conditions experienced by a given BY during the fall and spring preceding their outmigration. Scree plots were used to determine the number of principal components (PC) to retain by visually examining for steep drop-offs in the variance explained by each PC (Quinn and Keough 2002). Retained PCs were used to explain variance in log-transformed freshwater overwinter survival and smolt abundance by fitting multiple regression models.

The assumptions of multiple regression analyses (i.e., normality, constant variance, and independence of errors) were tested using residuals obtained from the fitted models (Quinn and Keough 2002). Normal probability plots were examined for one-to-one relationships between residuals and their theoretical to assess the assumption of normality. The assumption of constant variance was assessed by looking for even spread of residuals across the range of fitted values. Finally, autocorrelation plots were examined to determine if residuals from the fitted model were independent (i.e., lacked temporal autocorrelation). No violations of any of the previously mentioned assumptions were found. All statistical analyses were performed using R (R Core Team 2014).

Results

Over the time series, the mean BY overwinter survival rate of Unuk River Chinook Salmon was 53%, and ranged from 26% for the 2005 BY to 74% for the 1993 BY. There was no significant temporal trend in freshwater overwinter survival ($R^2 = 0.22$; $P = 0.09$); however, the overwinter survival of recent BYs was more likely to fall below the long-term mean value (Figure 2.2). The mean smolt abundance was 338,008 smolts and ranged from 165,253 smolts in the 2005 BY to 754,009 smolts in the 2006 BY.

Mean parr length and weight were 63.6 mm (range, 58.6 – 69.2 mm; SE = 3.3) and 3.0 g (range, 2.3 – 3.8 g; SE = 0.42), respectively (Figure 2.2). Both parr length ($R^2 = 0.41$; $P < 0.01$) and parr weight ($R^2 = 0.28$ $P = 0.04$) declined over the time series, which mirrored simultaneous increases in parr abundance ($R^2 = 0.40$; $P = 0.02$; Figure 2.2). Parr abundance explained significant variability in parr length ($\beta < -0.001$; $R^2 = 0.40$; $P = 0.02$) but not parr weight ($\beta < -0.001$; $R^2 = 0.27$; $P = 0.06$).

Mean fall temperature was 5.8 °C, and ranged from 3.5 °C in 2006 – 7.2 °C in 2002. Spring temperature had a mean value of 4.5 °C (range, 1.8 – 6.8 °C). Average fall and spring discharge was 1,040 m^3/s (range, 688 – 1,580 m^3/s), and 397 m^3/s (range, 190 – 1052 m^3/s), respectively. There were no significant trends in fall or spring discharge throughout the time series.

Multicollinearity among biotic and abiotic factors allowed their dimensions to be reduced using PCA. However, intermediate-loading values of the PCs made interpretation difficult; therefore, a varimax rotation was conducted to produce PCs that loaded primarily on biotic or abiotic factors. The varimax rotation resulted in the elimination of intermediate loading values

and a separation of biotic and abiotic factors (Table 2.1). The first PC loaded positively on spring and fall discharge and spring temperature (Table 2.1). The second PC loaded positively on biological factors (e.g., parr weight and length; Table 2.1), while the third PC loaded primarily on fall temperature (Table 2.1).

All three rotated PCs were used to explain variation in smolt abundance. This fitted model indicated that there were no relationships between any of the PCs and smolt abundance (Table 2.2). Another model was fitted using the PC with the regression coefficient that had the highest absolute value (PC 1). This model did not find a relationship between PC1 and smolt abundance ($R^2 = 0.23$; $P = 0.07$; Table 2.2).

Another multiple regression model was fitted using the three PCs as explanatory variables and freshwater overwinter survival as the response variable. All three PCs explained little variation in freshwater overwinter survival (Table 2.2). A reduced model that was fitted using only the second PC also explained little variation in freshwater overwinter survival of Unuk River Chinook Salmon (Table 2.2).

Discussion

In this study, PCA was conducted in conjunction with PCR to determine the relative influence of biotic and abiotic factors on the freshwater overwinter survival and smolt production of Chinook Salmon in the Unuk River. No significant relationships were found between any of the retained PCs and freshwater overwinter survival or smolt production. However, moderate amounts of variation in smolt production were explained by fall and spring discharge and spring air temperature, which indicated that abiotic factors have a greater impact regulating Chinook

Salmon smolt production than biotic factors in the Unuk River.

Previous research has indicated that annual discharge may influence the survival and productivity of Atlantic and Pacific salmon stocks (Gibson and Myers 1988; Cunjak et al. 1998; Neuswanger et al. 2015). For example, low winter flows have been associated with reduced survival of Atlantic Salmon (Gibson and Myers 1988; Cunjak et al. 1998). Cunjak et al. (1998) found a positive relationship between mean winter discharge and the interannual survival of age 0+ to 1+ and 1+ to 2+ Atlantic Salmon. The authors speculated that the relationship between discharge and survival may have been mediated by habitat availability, with low winter flows leading to reductions in overwinter habitat and, consequently, survival. The results of the current study suggested the opposite effect of discharge on survival with low spring and fall discharge leading to high smolt production. Other studies have indicated a negative effect of discharge on the survival of Chinook Salmon stocks in Alaska. For example, there was a negative relationship between summer discharge and the productivity of Chinook Salmon stocks in the Yukon River drainage (Neuswanger et al. 2015). The authors proposed that high discharge reduced the foraging efficiency of drift-feeding salmonids. High water velocity, turbidity, and in-river debris may lead Chinook Salmon to target debris as prey items, which in turn, may lower their energy intake rate. Further, increased water velocity could limit available foraging habitat, which, in combination with reduced energy intake rates, may cause fish to undertake risky behaviors (i.e., greater movements within the system) and increase their exposure to predators (Neuswanger et al. 2015).

Survival and production of Pacific salmon during freshwater residence may also be influenced by other abiotic factors such as water temperature. In the current study, high spring air temperatures were associated with reduced smolt production. Negative relationships between

air temperature and smolt production have been found for other species of Pacific salmon. For example, Lawson et al. (2004) found an inverse relationship between annual air temperature during the first year of freshwater residence and smolt production of Coho Salmon in northern and central Oregon. High temperatures increase the basal metabolic rates of poikilothermic organisms and, without concurrent increases in food availability, may lead to reductions in body condition and survival (Elliott 1988). In addition, large changes in temperature may increase acclimation costs, which, could lead to energy deficits and lower survival rates (Cunjak et al. 1987, 1988). For example, immature Brook Trout *Salvelinus fontinalis* and Brown Trout *Salmo trutta* exhibited depleted lipid reserves during late winter (February – March), with this depletion being most pronounced following the coldest winter (Cunjak 1988). Because energy reserves of salmonids are often depleted during the overwinter period (Cunjak et al. 1987), high spring temperatures could further deplete these reserves and lead to mortality (Cunjak 1988; Finstad et al. 2004). Future research should focus on developing a better understanding of how temperature influences food availability and the condition and survival of Pacific salmon during freshwater residence.

Biotic factors such as juvenile body size influences the mortality dynamics of salmonids during freshwater residence (Quinn and Peterson 1996; Meyer and Griffith 1997; Biro et al. 2004; Johnston et al. 2005). Previous research indicated that large body size may provide a survival advantage due to reduced risk of mortality via predation (Sogard 1997; Hurst 2007) and during periods of low food availability (Biro et al. 2004; Hurst 2007; Brown et al. 2011). Despite these size advantages for large fish, parr body size did not explain significant amounts of variation in the freshwater overwinter survival or smolt production of Unuk River Chinook Salmon. Multiple studies have similarly not detected a survival advantage for large-bodied

juvenile salmonids (Lund et al. 2003; Finstad et al. 2004; Carlson et al. 2008; Siikavuopio et al. 2009). The lack of a relationship between body size and freshwater overwinter survival may be the result of survival being more strongly related to energy levels within individual fish than mean body size of cohorts (Finstad et al. 2004). In turn, this relationship may also be dependent on environmental conditions (Meyer and Griffith 1997; Good et al. 2001). Meyer and Griffith (1997) compared the first-winter survival of large-bodied (> 90 mm) and small-bodied (< 90 mm) Rainbow Trout at warm and cold sites. At warm sites, survival was not related to body size; however, at cold sites, large-bodied fish had significantly higher survival than small-bodied individuals. Good et al. (2001) examined the relationship between Atlantic Salmon body size and survival over two consecutive years and found that large-bodied individuals had a survival advantage during a summer characterized by drought conditions while small-bodied individuals had higher survival during a summer with multiple flood events. Therefore, the relationship between body size and survival appears to be complex and may depend on local environmental conditions. Future research should focus on developing a better understanding of how body size and environmental conditions interact to determine the survival and smolt production on Pacific salmon in freshwater systems.

Climate change may alter freshwater systems, which in turn, may influence smolt production and freshwater survival of Chinook Salmon in SEAK. As a region, SEAK is thought to be particularly sensitive to climate change due to its near freezing winter air temperatures (-4^{o}C; Simpson et al. 2005). Small changes in ambient air temperatures could change precipitation from snow to rain and increase glacial melt, which may have large-scale impacts on the flow and temperature regimes of freshwater systems within the region. Model simulations suggest that freshwater systems within this region may experience higher spring and fall discharge and as

well as winter water temperatures (Bryant 2009; Fellman et al. 2015; Shanley and Albert 2014). The results of the current study suggest that these changes may lead to lower Chinook Salmon smolt production within the Unuk River.

The current study highlights the need for local data to better characterize the role of abiotic factors in determining the freshwater overwinter survival of Chinook Salmon in the Unuk River. Chinook Salmon are thought to overwinter in side channels of this system after migrating from their natal streams in the summer and fall (P. Richards, ADF&G, personal communication). However, there is currently a lack of indexed abiotic data in these areas during the overwinter period. While air temperature has been used as a proxy of stream temperature in rain-fed systems in the Pacific Northwest (Lawson et al. 2004), the relationship between air and water temperatures is weaker for glacially influenced systems in SEAK (Fellman et al. 2014). In addition, salmonids may select microhabitats that serve as thermal refuges during the overwinter period (Hurst 2007); therefore, the abiotic data used in this study may not accurately represent water temperatures during the overwinter period or have had too coarse of a resolution to detect relationships with overwinter survival. The current study also lacked data relating to habitat availability, which has been shown to influence the overwinter survival of salmonids (Quinn and Peterson 1996; Hurst 2007; Brown et al. 2011). For example, Quinn and Peterson (1996) found a strong positive relationship between the amount of woody debris and the overwinter survival of Coho Salmon in Big Beef Creek, Washington. Chinook Salmon are often found in association with this habitat type during the overwinter period in the Unuk River (P. Richards, ADF&G, personal communication); therefore, quantifying the availability of woody debris in this system may lend insights into the factors that limit overwinter survival in this system.

While no significant relationships were detected between either biotic or abiotic factors and the freshwater survival or smolt production, average spring temperature and average spring and fall discharge may have a negative effect on Chinook Salmon smolt production in the Unuk River. However, there is currently a lack of understanding of the mechanisms that link these abiotic factors to smolt production within the system. Previous research suggests that high flow may inhibit the foraging efficiency of drift feeding salmonids (Neuswanger et al. 2015), which may explain the negative effect of fall and spring discharge on smolt production. In addition, warm spring water temperatures may increase basal metabolic costs and further deplete energy reserves after the overwinter period, which in turn, could lead to high mortality rates. Projected increases in winter water temperatures and fall and spring discharges in the region due to climate change could impact smolt production within this system. Overall, the current study provided insight into the factors potentially related to the overwinter survival and smolt production of Chinook Salmon in freshwater systems and may be used to guide future research in this area.

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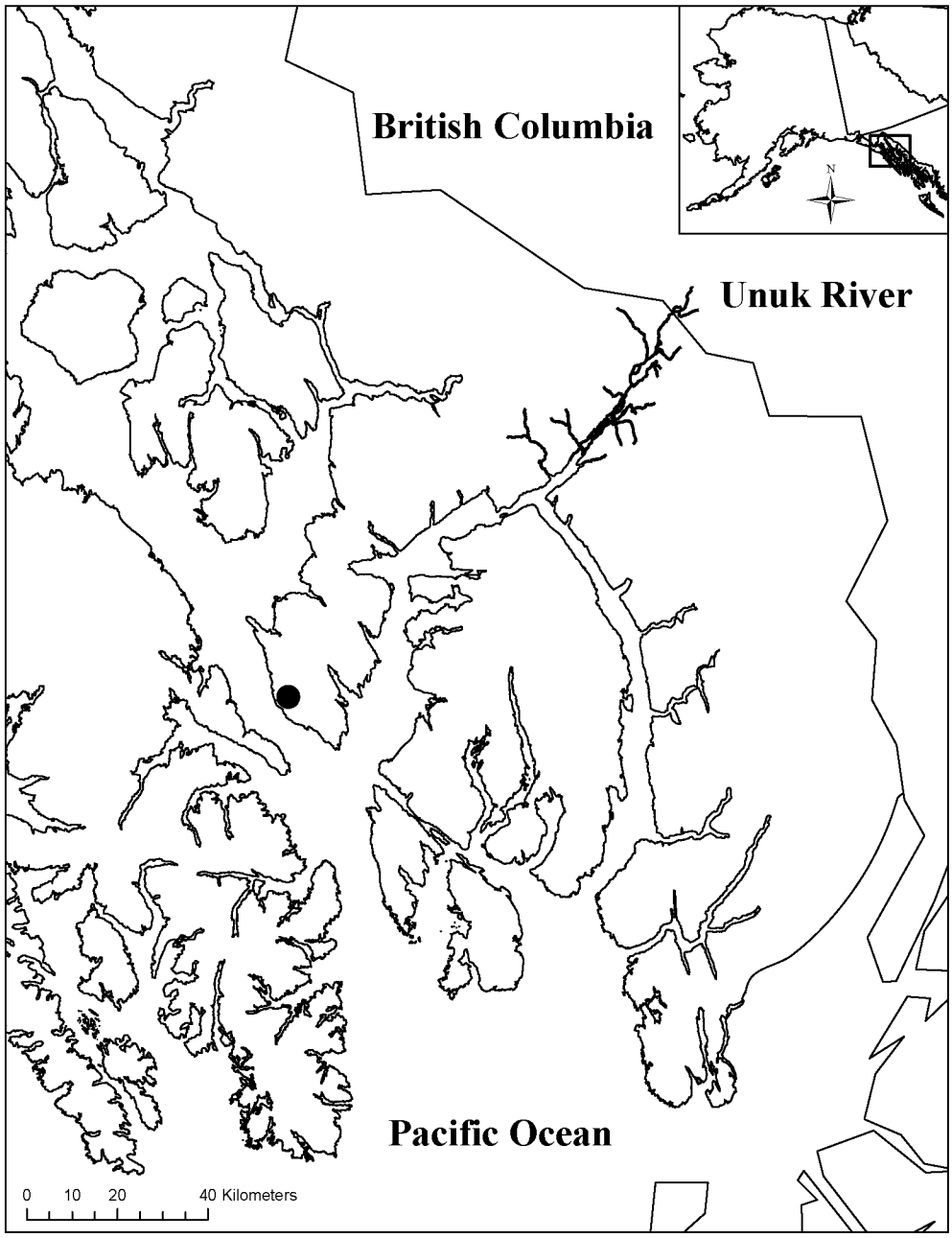

Figure 2.1. The Unuk River in Southeast Alaska and British Columbia. The bold line indicates the location of the Unuk River while the circle represents the location of National Weather Service weather station where the air temperature data were collected.

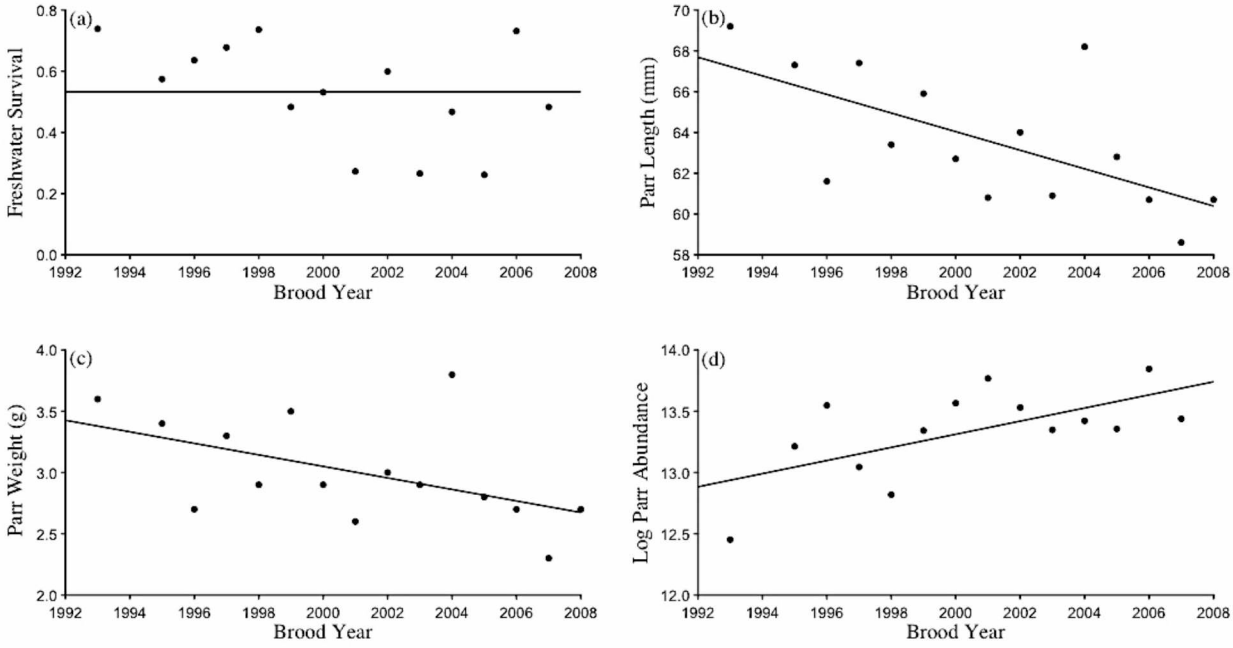

Figure 2.2. Time series of (a) freshwater overwinter survival, (b) mean parr length (mm), (c) mean parr weight (g), and (d) log-transformed parr abundance for brood years 1993 – 2008. The horizontal line in panel (a) represents mean freshwater survival during brood years 1993 – 2008. The lines in panels (b, c, d) were obtained by fitting simple linear regression models using brood year to explain variation in parr length, weight, and abundance.

Table 2.1. Loadings between rotated principal components and fall (October – November) and spring (March – April) mean temperature and discharge and mean parr weight and length.

	PC1	PC2	PC3
Fall temperature (°C)			0.987
Spring temperature (°C)	0.908		
Fall discharge (m^3/s)	0.766	0.115	0.119
Spring discharge (m^3/s)	0.896		-0.355
Parr length (mm)		0.986	
Parr weight (g)		0.984	

Table 2.2. Results of multiple and simple linear regression analyses that examined the relationships between rotated principal components and log-transformed smolt production and log-transformed overwinter survival of Unuk River Chinook Salmon.

		Model				
Dependent variable	Independent variable	β	Standard error	t-value	*P*-value	R-squared
Smolt production	PC1	-0.20	0.10	-1.89	0.09	0.09
	PC2	-0.08	0.10	-0.82	0.43	
	PC3	0.04	0.10	0.34	0.74	
Smolt production	PC1	-0.20	0.10	-1.98	0.07	0.23
Freshwater overwinter survival	PC1	-0.10	0.10	-0.94	0.37	-0.04
	PC2	0.13	0.11	1.19	0.26	
	PC3	0.06	0.10	0.59	0.57	
Freshwater overwinter survival	PC2	0.12	0.10	1.17	0.26	0.10

Chapter 3: Influence of smolt biological attributes and early marine conditions on the marine survival of Unuk River Chinook Salmon[1]

Abstract

Recent reductions in the run sizes of Chinook Salmon *Oncorhynchus tshawytscha* in Southeast Alaska have resulted in social and economic hardships within the region. Previous research suggests that Pacific salmon year-class strength may be determined by size-selective processes that occur during the early marine phase of their life cycle; however, the relative influence of freshwater growth, such as smolt body size, and early marine conditions on the marine survival of Chinook Salmon is unknown. Principal component analysis and principal component regression (PCR) were used in conjunction to determine the influence of early marine sea-surface temperatures (June – July index during year of outmigration) collected at three locations (Upper Chatham Strait, Icy Strait, and Auke Bay Monitor) and smolt biological attributes (i.e., length [mm], weight [g]), on brood year (1995 – 2008) marine survival of Unuk River Chinook Salmon. When all brood years were examined using PCR, there was a significant positive relationship between marine survival and sea-surface temperature in Upper Chatham Strait, Icy Strait, and Auke Bay Monitor ($P = 0.04$). When a PCR model was fitted using only brood years with below average marine survival, there were significant positive relationships between sea-surface temperatures in Upper Chatham Strait, Icy Strait, and Auke Bay Monitor and marine survival ($P = 0.01$) and smolt biological variables (i.e., length and weight) and marine survival ($P = 0.02$). The results of this study suggest that brood-year marine survival is regulated by

[1] Graham, C. J., T. M. Sutton, M. V. McPhee, M. D. Adkison, and P. J. Richards. 2016. Influence of smolt biological attributes and early marine conditions on the marine survival of Unuk River Chinook Salmon. Prepared for submission to Transactions of the American Fisheries Society.

oceanic conditions that occur during early marine residence and that large smolt body size may provide a survival advantage during brood years with poor marine survival.

Introduction

Chinook Salmon *Oncorhynchus tshawytscha* are socially, culturally, and economically important throughout their range (Der Hovanisian et al. 2011; Schindler et al. 2013). In Southeast Alaska (SEAK), Chinook Salmon are harvested in commercial, sport, and subsistence fisheries (Der Hovanisian et al. 2011). However, recent regional reductions in Chinook Salmon abundance and subsequent restrictions in catch limits have resulted in declines in sport fish landings and commercial harvests (Der Hovanisian et al. 2011). Because reduced harvests often lead to social and economic hardships, it is important to try to uncover the factors responsible for the current declines in the productivity and survival of salmon stocks within SEAK.

Previous research has indicated that size-selective processes during early marine residence may determine Pacific salmon *Oncorhynchus* spp. year-class strength (Beamish and Mahnken 2001; Farley et al. 2007). The critical-size, critical-period hypothesis proposes that salmon mortality is concentrated in two distinct periods during the first year at sea (Beamish and Mahnken 2001). The first period of high mortality is size mediated and occurs shortly after smolts enter the ocean. Smoltification is an osmotically stressful process that may lead to reduced predator avoidance and high mortality when entering predator-dense coastal environments (Handeland et al. 1996; Dieperink et al. 2002). Recent literature indicates that body size at ocean entry is positively related to marine survival in Pacific and Atlantic salmon *Salmo salar* (Kallio-Nyberg et al. 2004; Antonsson et al. 2010; Murphy et al. 2013). Large body size may reduce the risk of predation in two ways (Sogard 1997). First, large body size physically prevents predation due to gape limitations of predators (Sogard 1997; Juanes et al. 2002; Dörner and Wagner 2003). Second, swimming ability is positively related to body size;

therefore, larger fish are better able to escape potential predators than smaller individuals (Juanes 1994). The second period of high mortality for Pacific salmon is mediated by physiological processes and occurs during the first fall and winter at sea (Beamish and Mahnken 2001; Beamish et al. 2004). Similar to freshwater systems, the marine overwintering period is physiologically stressful; as a result, individuals that do not achieve sufficient body size during their first marine summer do not have sufficient energy stores to survive the metabolically demanding late fall and winter (Beamish and Mahnken 2001; Beamish et al. 2004; Biro et al. 2004; Farley et al. 2007). This "critical period" also has support in the literature; reconstructed scale growth histories indicate that fast-growing Coho Salmon *O. kisutch* were significantly more likely to survive their first marine winter than slower-growing members of the population (Beamish et al. 2004). Because size-selective processes mediate mortality during both periods, growth conditions during early marine residence may regulate brood-year survival of Chinook Salmon in SEAK.

Climate plays a profound role in shaping the structure and function of freshwater and marine ecosystems, which in turn, may affect salmon growth and survival directly through changes in water temperatures and indirectly through changes in bottom-up processes (Benson and Trites 2002; Mueter et al. 2002a; Edwards and Richardson 2004; Seo et al. 2006; Noakes and Beamish 2009; Petrosky and Schaller 2010; Hunt et al. 2011; Doney et al. 2012; Shanley and Albert 2014; Wobus et al. 2015). Multiple studies have linked variations in sea-surface temperature (SST) and Pacific salmon survival at regional and basin-wide scales (Mueter et al. 2002a, 2005; Stachura et al. 2014; Miller et al. 2014). For instance, regional SSTs experienced shortly after entering the marine environment influenced the survival rates for both northern (i.e., Alaska) and southern stocks (i.e., British Columbia and Washington) of Pacific salmon (Mueter

et al. 2002a, 2005). Climate may also influence the survival of Pacific salmon indirectly through changes in the timing and availability of primary and secondary production and changes in food-web structure (Edwards and Richardson 2004; Hertz et al. 2016). Variations in long-term abundance trends of Pacific salmon from large regions in the North Pacific Ocean have tracked changes in large-scale climate indices such as the Pacific Decadal Oscillation (PDO; Hare and Mantua 2000) and the Aleutian Low Pressure Index (ALPI; Beamish and Bouillon 1993; Noakes and Beamish 2009; Stachura et al. 2014). Thus, the non-static nature of climate and its regulation of the processes that influence the growth and recruitment success of Pacific salmon may explain long-term fluctuations in the abundance and survival of Chinook Salmon stocks in SEAK.

While smolt body size and oceanic conditions during early marine residence have been found to influence Pacific salmon year-class strength, the relative influence of these variables and their importance in driving the current declines in survival of Chinook Salmon in SEAK is unknown. The objective of this study was to assess the relationship between Chinook Salmon smolt biological attributes (i.e., smolt length and weight) and early marine environmental conditions (i.e., regional SSTs) on the marine survival of Unuk River Chinook Salmon. In this study, principal component analyses and principal component regression were used in conjunction to test two null hypotheses: 1) there is no correlation between marine survival of Unuk River Chinook Salmon and environmental variables during early marine residence; and 2) marine survival of Unuk River Chinook Salmon is not positively related to smolt body size. These study results will contribute to the understanding of the factors that influence the marine survival of SEAK Chinook Salmon stocks.

Methods

Study site

The Unuk River is a glacially influenced, transboundary system that originates in British Columbia and empties into Behm Canal approximately 85 km east of Ketchikan in SEAK (Figure 3.1; Hendrich et al. 2008). The system was chosen for this study for multiple reasons. First, the Unuk River is, on average, the fourth-largest producer of Chinook Salmon within SEAK, with annual runs of approximately 5,500 large fish (> 660 mm) per year (Der Hovanisian et al. 2011). Second, due to its importance in regional salmon production, this system has a long-term Alaska Department of Fish and Game (ADF&G) stock assessment program in place (1993–present; Hendrich et al. 2008). Finally, proposed, large-scale mining development threatens pristine spawning and rearing habitats of Chinook Salmon on the Unuk River (Pahlke et al. 1995; Canadian Environmental Assessment Agency 2014). For example, the Kerr-Sulphurets-Mitchell mine (KSM) is a proposed transboundary, open-pit mine located on Sulphurets Creek in northern British Columbia, which is a tributary of the Unuk River. As planned, KSM will be similar in scale to the proposed Pebble Mine. Due to its large size, over 450,464 L of contaminated water per minute will be treated prior to storage in a 165 m tall earthen dam (Canadian Environmental Assessment Agency 2014). The location of the proposed KSM dam and the long-term storage of waste threatens pristine spawning and rearing habitat for Chinook Salmon and other Pacific salmon stocks. It is estimated that approximately 83% of Chinook Salmon from the Unuk River spawn downstream from the Canadian border (Pahlke et al. 1995). Therefore, large segments of Unuk River Chinook Salmon are susceptible to the proposed development.

Unuk River Chinook Salmon are predominately "stream-type", spending one year in freshwater prior to entering the marine environment as two-year-old smolts (Quinn 2005; Hendrich et al. 2008). Smolts from this system migrate to the ocean between late March and early May. Previous research indicates that Unuk River Chinook Salmon rear primarily within the inside waters of SEAK and British Columbia for one to five years before returning to the Unuk River to spawn as mature adults (Hendrich et al. 2008; Der Hovanisian et al. 2011).

Biological data

The ADF&G Unuk River coded-wire tag (CWT; 1992 – present) and mark-recapture program (1997 – present) allowed the estimation of smolt biological attributes (i.e., fork length [mm] and weight [g]) and marine survival of Unuk River Chinook Salmon (brood years [BY] 1992–2008; Hendrich et al. 2008; Weller and Evans 2012). Subsequent BYs (i.e., 2009 – present) were not included in these analyses because all Chinook Salmon from these BYs have yet to return from the ocean; therefore ADF&G has not estimated their marine survival.

Smolt length and weight

Chinook Salmon smolts were captured by ADF&G using minnow traps (420 mm long × 191 mm diameter, with 6-mm mesh) baited with salmon roe in back eddies and major sloughs of the lower portion of the Unuk River during smolt outmigration from late March through early May (Hendrich et al. 2008; Weller and Evans 2012). All captured smolts ≥ 50 mm fork length (FL) that were not missing an adipose fin were implanted with a coded-wire tag (CWT) and marked by excising their adipose fin for future identification. Annual systematic subsamples of 138

smolts were measured to the nearest 1 mm and weighed to the nearest 1 g to estimate the mean length and weight of the populations with 95% relative precision.

Smolt abundance

The BY abundance of Unuk River Chinook Salmon smolt was estimated by the ADF&G using a two-event mark-recapture experiment using a modified Chapman-Petersen formula (Seber 1982; Weller and Evans 2012). In the first event, smolts were implanted with CWTs and marked as previously described. In the second event, adults were sampled on the spawning grounds when estimating the inriver abundance of mature Chinook Salmon. Because the proportion of adults from a BY with coded-wire tags did not vary considerably over return years (Weller and Evans 2012), the number of adults with adipose fin clips were used to estimate the ratio of marked and unmarked fish in the second event.

Adult abundance, total return, and marine survival

The inriver run of large (≥ 660 mm) and small (< 660 mm) adult Unuk River Chinook Salmon, BY 1995–2008, was estimated using two-event mark-recapture experiments (Hendrich et al. 2008; Weller and Evans 2012). In the first event, Chinook Salmon were marked after being captured with set gill nets (37 m long × 4 m deep, with 1.8-mm stretch mesh) approximately 3 km upstream of the ocean entry point on the mainstem of the Unuk River. All captured fish were sampled to determine the age, sex, and length (ASL) composition of the inriver run. All fish that were not missing their adipose fin and determined to be in good condition were marked using solid-core spaghetti tags. A left upper operculum punch (0.63 cm in diameter) was also used as a secondary mark to assess tag retention rates. In the second event, fish were visually

examined for marks after being captured using rod and reel, dip nets, gill nets, and carcass surveys on the spawning grounds. Each captured fish was inspected for presence of a spaghetti tag, left upper operculum punch, and missing adipose fin. After mark inspection, ASL data were collected and a lower left operculum punch was used to prevent double sampling. Abundances of large and small adult Chinook Salmon were estimated separately by the ADF&G using a modified Chapman-Petersen estimator (Seber 1982).

Total return was calculated as the sum of estimated inriver run and marine harvest for 1.2 to 1.5 age fish within a given BY. Abundance by age class was estimated using the estimated abundance of small and large fish and size-composition data from the spawning ground surveys. The marine harvest of Chinook Salmon in regional commercial and sport fisheries was estimated following the methods described by Bernard and Clark (1996). Finally, BY marine survival was estimated by ADF&G as the ratio of BY total return and BY smolt abundance.

Physical data

A time series of SSTs (^{o}C; 1997 – 2015) was received from the National Oceanic and Atmospheric Administration (www.noaa.gov). The provided data were collected as part of the Southeast Alaska Coastal Monitoring project which was initiated in 1997 to study the distributions and early marine ecology of juvenile salmon in coastal waters of the Gulf of Alaska ecosystem (Orsi et al. 1997). Sea-surface temperature data were collected at three locations: Upper Chatham Strait, Icy Strait, and Auke Bay Monitor using an conductivity-temperature-depth profiler that measured SSTs at 3 m depth (Figure 3.1). Stations within Upper Chatham Strait and Icy Strait were included because they are located along a potentially important overwintering location and migration corridor for Pacific salmon in SEAK (Orsi et al. 2013).

However, Orsi et al. (2000) indicated that juvenile Chinook Salmon were more abundant in inshore habitats near Auke Bay Monitor than in Upper Chatham Strait and Icy Strait. Four stations were sampled in both Upper Chatham Strait and Icy Strait and one station was measured in Auke Bay Monitor (Table 3.1; Figure 3.1). While the mouth of the Unuk River was approximately 375 km from Icy Strait, previous research indicates that survival of Pacific salmon stocks were significantly correlated with SSTs located 400 km from their ocean entry point (Mueter et al. 2002a).

An index of early summer SSTs was created at each location by averaging June and July water temperatures for all stations within that location. This index was chosen because processes that occur during the early marine residence are thought to affect the survival of Pacific salmon (Mueter et al. 2002a; Quinn 2005). The time period of this index was applicable because Unuk River Chinook Salmon do not complete their outmigration until early to mid May (Hendrich et al. 2008). While basin-scale indices (e.g., PDO, ALPI, etc.) have been shown to explain variation in the catches/survival of multiple species of Pacific salmon, these indices were not included these in these analyses because Unuk River Chinook Salmon rear primarily in inside waters in SEAK (Beamish and Bouillon 1993; Mantua et al. 1997; Hendrich et al. 2008; Der Hovanisian et al. 2011); therefore, the use of regional measures of climate was considered more appropriate. All physical data were lagged two years (brood year + 2) to represent early ocean conditions during the year of smolt outmigration. Because the Southeast Alaska Coastal Monitoring project was not initiated until 1997 (1995 BY), subsequent data analyses were performed using marine survival and smolt biological data from the 1995 – 2008 BYs.

Data analyses

Due to high correlations among explanatory variables and the low number of observations (n = 14) per explanatory variable (n = 5), the relationship between marine survival and the biotic and abiotic factors was analyzed using principal component analysis (PCA) and principal component regression (PCR). The biotic (smolt length [mm] and weight [g]) and abiotic (water temperature [^{o}C; June – July average]) variables were entered into separate matrices and their dimensions were reduced by conducting PCA on each of the separate matrices (R; function: prcomp; package: stats; R Core Team 2014). Conducting PCA separately on biotic and abiotic factors led to better separation of these variables and more interpretable components than when PCA was conducted using both biotic and abiotic factors. The number of PCs that were retained was determined by examining the proportional variance explained by each PC (Quinn and Keough 2002). After retaining the PCs that explained the most variation in predictor variables, a multiple regression model was fitted using PC scores to explain variance in log-transformed marine survival. Previous research indicated that size at ocean entry may be more important in influencing survival during years of poor recruitment (Holtby et al. 1990; Woodson et al. 2013). Therefore, a separate multiple regression model was fitted using BYs with below-average marine survival. Mean marine survival was calculated using the entire time series and BYs, with below-average survival were used to create a time series that represented years of poor recruitment. Principal component scores for years that corresponded to BYs with below average marine survival were extracted used to describe variance in log-transformed marine survival.

The assumptions of multiple regression (i.e., normality, constant variance, and independence of errors) were tested using residuals obtained from the fitted models. The assumption of normality was assessed visually by examining normal probability plots (R;

function: qqnorm; package: stats) for one-to-one relationships between residuals and their theoretical values. The assumption of constant variance was also visually assessed by looking for even spread of residuals across the range of fitted values. Neither assumption was violated for either of the fitted multiple regression models. Multiple regression models also assume linear relationships between predictor and response variables. Bivariate scatterplots were used to determine the nature of the relationships between response and explanatory variables; no transformations of explanatory variables were needed to meet this assumption. Parameters in this model were estimated using least-squares regression, and all statistical analyses were carried out at alpha = 0.05 level using R (R Core Team 2014).

Results

Over the time series, marine survival of Unuk River Chinook Salmon averaged 2.5% and ranged from 0.7% for the 2006 BY to 4.6% for the 2005 BY. There was no significant trend in log-transformed marine survival across the time series (β = -0.05, P = 0.14); however, the marine survival of recent BYs (2003 – 2008) were more likely to fall below the long-term average of the time series than previous BYs (1995 – 2002; Figure 3.2).

Mean smolt length and weight at ocean entry were 68.1 mm (SE = 2.1; range, 64.8 – 71.5 mm), and 3.3 g (SE = 0.35; range, 2.7 – 3.8 g), respectively. There were no significant trends in any of the smolt attributes over time. In BYs with above-average marine survival, there were no clear relationships between average BY smolt length and marine survival (Figure 3.3). However, when BY marine survival was below average, there was a positive linear relationship between average smolt length and BY marine survival (Figure 3.3).

Mean June and July water temperatures were highest at Auke Bay Monitor (12.4 °C), followed by Upper Chatham Strait (11.9 °C) and Icy Strait (11.8 °C). Overall, the range and SE in mean temperatures were similar for each station (Auke Bay Monitor [SE = 0.83, range, 10.5 – 13.5 °C], Upper Chatham Strait [SE = 0.75; range, 10.6 – 13.0 °C], and Icy Strait [SE = 0.80; range, 10.5 – 13.2 °C]). Mean June and July SSTs were highly correlated for Upper Chatham Strait and Icy Strait (r = 0.92) and moderately correlated for Auke Bay Monitor and Upper Chatham Strait (r = 0.67) and Auke Bay Monitor and Icy Strait (r = 0.66). There were no significant trends in temperature at any station across the time series.

The high correlations among biotic and abiotic factors led to a reduced dimensionality of these variables in the separate PCA analyses. For the biotic factors, the first PC (PC1.bio) explained the majority of variation in smolt body size and loaded negatively on smolt length and weight (Table 3.2). The first two PCs (PC1.abio and PC2.abio) explained the majority of variability in the abiotic factors, with PC1.abio loading on SSTs from all three locations and PC2.abio loading primarily on SSTs from Auke Bay Monitor (Table 3.3). Because the first PC1.bio explained the variability in smolt body size, and PC1.abio and PC2.abio explained the majority of variation in SSTs they were retained for the subsequent analyses.

A multiple regression model that was fitted using all three retained components (PC1.bio, PC1.abio, and PC2.abio) indicated that there was a positive relationship between SSTs in Upper Chatham Strait, Icy Strait, and Auke Bay Monitor and marine survival (Figure 3.4). While the regression coefficient for PC1.bio had a similar absolute value to PC1.abio, PC1.bio was not significantly related to marine survival (Figure 3.4). Overall, these three components explained 22% of the variation in marine survival. When only examining BYs with below average marine survival, both PC1.bio and PC1.abio were significantly related to marine survival, which

indicated that both smolt body size and SSTs in Upper Chatham Strait, Icy Strait, and Auke Bay Monitor were positively related to marine survival for brood years that experienced poor marine survival (Figure 3.4). The principal components explained more variation ($R^2_{adj} = 0.70$) in marine survival during BYs with low marine survival than did the model that was fitted with all of the BYs ($R^2_{adj} = 0.22$).

Discussion

Results of this study suggested that marine survival of Unuk River Chinook Salmon was affected by oceanographic conditions (i.e., SST) during their first few months at sea. While Chinook Salmon have been documented in waters near Upper Chatham Strait, Icy Strait, and Auke Bay Monitor, there is currently a poor understanding of stock-specific early marine distributions of Chinook Salmon in the region (Orsi et al. 2013). Because of the spatial correlation of coastal SSTs in the North Pacific Ocean, it was not possible to determine if marine survival was influenced by conditions in these sampling locations or by similar conditions in another part of the region (Mueter et al. 2002b). In contrast, only moderate support was found for the influence of smolt biological attributes on the survival of Unuk River Chinook Salmon. However, the relationship between smolt body size and marine survival was more apparent in BYs with below average survival; therefore, the relationship between smolt body size and survival may depend on other factors such as growth conditions during the first few months at sea.

Interannual variations in the marine survival of Unuk River Chinook Salmon may be described by coastal marine conditions during their first few months at sea. This finding is congruent with the current literature that proposes Pacific salmon year-class strength is

determined during early marine residence (Beamish and Mahnken 2001; Farley et al. 2007). For example, it has been estimated that 53 – 94% of Pink Salmon *O. gorbuscha* may perish during their first 40 – 45 days at sea (Karpenko 1998). While Karpenko (1998) did not directly determine the cause of Pink Salmon mortality, high mortality of Pacific salmon during the first few months at sea is often attributed to size-dependent processes such as predation (Quinn 2005); therefore, high growth during early marine residence may increase survival (Sogard 1997; Beamish and Mahnken 2001). Miller et al. (2014) reported that increases in early ocean growth and body size after twenty days at sea were associated with higher marine survival of Snake River Chinook Salmon. Positive relationships between growth and marine survival have also been found for Coho Salmon (Beamish et al. 2004), Pink Salmon (Moss et al. 2005), and Sockeye Salmon *O. nerka* (Ruggerone et al. 2007). Therefore, oceanic conditions that regulate growth during early marine residence may be important in determining the marine survival of Pacific salmon.

Temperature may affect the growth of fish directly through changes in metabolic rates and indirectly through changes in the structure and function of ecosystems (Groot et al. 1995; Hunt et al. 2011). The results of this study found a significant positive relationship between Unuk River Chinook Salmon marine survival and SSTs in Upper Chatham Strait, Icy Strait, and Auke Bay Monitor which are potentially important rearing locations for Chinook Salmon in SEAK (Orsi et al. 2013). Higher survival of Pink, Sockeye, and Chum Salmon *O. keta* in SEAK has also been associated with warm coastal oceanic conditions (April – July) during their first year at sea (Mueter et al. 2002a, 2005). In contrast, survival of California and British Columbia stocks of Pacific salmon (i.e., Chinook, Pink, Sockeye and Coho Salmon) is often higher in years characterized by colder than average SSTs (Koslow et al. 2002; Mueter et al. 2002a, 2005; Miller

et al. 2014). The opposite effect of SST on survival of northern and southern stocks suggests that SSTs affect Pacific salmon survival indirectly through mechanisms that regulate biological production (Koslow et al. 2002; Mueter et al. 2002a; Logerwell et al. 2003; Hertz et al. 2016). Mueter et al. (2002a) noted that the relationship between Pacific salmon survival and SSTs changed near the boundary separating the upwelling-dominated southern region and the downwelling-dominated northern region. The processes that regulate biological production in the southern upwelling-dominated region are fairly well known. For example, cold SSTs are associated with increased upwelling, primary production, and abundances of lipid-rich copepod species off the coast of Oregon and Washington, which in turn, are correlated with higher abundances of forage-fish species and increased marine survival of Pacific salmon (Koslow et al. 2002; Peterson and Keister 2003).

While there is a basic understanding of the processes that regulate Pacific salmon production in the southern portion of their range, the mechanisms that regulate biological productivity in SEAK are not well understood. Increases in SSTs may lead to higher water column stability via thermal stratification, which has been associated with increases in overall primary production in the Gulf of Alaska (Gargett 1997). Regional changes in freshwater discharge may also affect SSTs and nutrient availability in the Gulf of Alaska Ecosystem via accelerations in the Alaska Coastal Current; these accelerations have been linked to influxes of warm, nutrient-rich southern waters (Royer et al. 2001). Regional SSTs have also been found to influence zooplankton species assemblages, forage-fish distributions, and the diets, condition, and size of Pacific salmon (Abookire et al. 2000; Mackas et al. 2001; Farley et al. 2007; Fergusson et al. 2013). For example, Abookire et al. (2000) found that forage-fish species distributions in Cook Inlet, Alaska, were linked to spatial differences in water stratification, with

schooling fish more likely to inhabit well-stratified waters. In addition, the body size (i.e., weight and length) of Pink, Chum, and Coho Salmon were found to be significantly larger in years characterized by warm versus cold SSTs (Fergusson et al. 2013). While variations in species assemblages and distributions and the size of Pacific salmon in warm versus cold years may explain the indirect relationship between SSTs and Chinook Salmon survival, there is a clear need for a better understanding of the mechanisms that link changes in oceanic conditions to Pacific salmon productivity in SEAK.

While previous studies have examined the influence of early ocean conditions on the survival of Pacific salmon, the current study also examined the importance of smolt biological attributes in determining marine survival (Mueter et al. 2002a, 2005; Koslow et al. 2002). The results of the current study indicate that smolt body size and weight accounted for less variation in the survival of Unuk River Chinook Salmon than did SSTs during early marine residence. Large body size has been found to reduce size-selective mortality of Pacific and Atlantic salmon smolts during their early marine residence (Jutila et al. 2006; Woodson et al. 2013). For example, Jutila et al. (2006) found a significant, positive relationship between mean annual smolt length and weight and marine survival of Atlantic Salmon. Higher survival of large smolts has been attributed to gape limitations in predators and the positive relationship between body size and swimming ability, which allows large-bodied fish to better escape potential predators than their small-bodied conspecifics (Sogard 1997). However, the relationship between body size and survival may be dependent on cohort survival or conditions experienced during early marine residence (Woodson et al. 2013).

The current study found support for a survival advantage related to the body size (i.e., weight and length) of Unuk River Chinook Salmon smolts; however, this survival advantage was

more pronounced during BYs with below average recruitment success. Previous research that examined the influence of smolt body size on survival also indicated that smolt length does affect survival, but only in years characterized by poor survival (Holtby et al. 1990; Blom et al. 1994; Woodson et al. 2013). For example, Chinook Salmon from California's Central Valley experienced size-selective mortality at ocean entry in years of low, but not high, recruitment (Woodson et al. 2013). Holtby et al. (1990) examined the relationships between smolt length, early marine growth, and marine survival of Coho Salmon in British Columbia and found marine survival was positively related to both early marine growth and smolt length; however, the survival advantage of large-bodied smolts was only apparent in years with low overall survival. Further, both marine survival and early ocean growth were enhanced during years characterized by strong upwelling along the coast of Vancouver Island, British Columbia, which led the authors to speculate that favorable oceanic and growth conditions might have allowed small smolts to quickly grow out of size classes susceptible to predation. Therefore, BYs that encountered favorable early ocean conditions may have obscured the survival advantage of large smolts by allowing small individuals to grow at faster rates and experience reduced amounts of size-dependent mortality.

While the results of the current study highlight the importance of freshwater growth in determining the marine survival of Unuk River Chinook Salmon, climate change and proposed development within the region could alter freshwater growth rates. The Unuk River is located within SEAK, which is thought to be a region that is particularly sensitive to climate change due to its near freezing winter air temperatures (-4°C; Simpson et al. 2005). Therefore, while other regions may face higher changes in air temperatures, smaller changes in ambient air temperatures in SEAK may have profound impacts on freshwater ecosystems (ACIA 2004). For example,

small increases in air temperature could change winter precipitation from snow to rain, which in turn could affect flow regimes and potentially the rearing locations of Pacific salmon (Shanley and Albert 2014). Currently, there is limited understanding of how changes in climate and rearing locations could affect the growth rates Pacific salmon in SEAK. Glacially fed systems like the Unuk River could face colder water temperatures during the summer due to increased glacial melt and increased winter air temperatures (Fellman et al. 2015), with resulting declines in temperatures potentially reducing Chinook Salmon growth through lower metabolic rates (Groot et al. 1995). Increased winter water temperatures may also reduce growth rates and body condition through increased basal metabolic costs in food-limited environments (Groot et al. 1995; Sandersfeld et al. 2015). In addition to climate change, proposed development within the Unuk River drainage could degrade rearing habitats and alter growth rates (Bash et al. 2001). For example, the Kerr-Sulphurets-Mitchell mine is a proposed large-scale open pit mine located on the Unuk River in Northern British Columbia (Canadian Environmental Assessment Agency 2014). One potential consequence of this proposed mining project is increased levels of selenium within the Unuk River Watershed, which in turn, may affect the growth and survival of Chinook Salmon (Canadian Environmental Assessment Agency 2014). While selenium is an essential micronutrient for plants and animals, it has toxic affects at slightly higher than required concentrations (Hilton et al. 1980). For example, Chinook Salmon that were fed diets high in selenium experienced reduced growth and survival relative to a low-selenium control group (Hamilton et al. 1990). Therefore, potential development and climate change may lead to reductions in Unuk River Chinook Salmon smolt body size and marine survival.

While the current study demonstrated that marine survival of Unuk River Chinook Salmon is positively related to Upper Chatham Strait, Icy Strait and Auke Bay Monitor SSTs and

smolt body size, the analysis of a single stock precludes regional generalizations of the influence of these factors on the current declines in Chinook Salmon abundance, productivity, and survival in SEAK. Smolt abundances of Chinook Salmon stocks within the region vary considerably, which in turn may affect the intensity of size-selective predation (Hendrich et al. 2008; McPherson et al. 2010; Chapell and Elliott 2013; Cunningham et al. 2013). Therefore, the influence of body size at ocean entry may depend on stock-specific characteristics. Future research should employ a multi-stock approach to assess whether the results of this study can be applied to stocks across the region. Another limitation of this study was the lack of data relating to the early ocean growth of Unuk River Chinook Salmon, which precluded the assessment of the relative influence of early marine growth versus smolt body size in determining marine survival. Even when considering the aforementioned limitations of this research, this study provided valuable information on the relationships between smolt biological attributes and early ocean conditions on the marine survival of a regionally important salmon stock.

The results of the current study indicated that marine survival of Unuk River Chinook Salmon is positively related to SSTs located within a potentially important overwintering area for Chinook Salmon in SEAK. However, there is currently a lack of understanding of the specific mechanisms that drive this observed relationship between SSTs and survival. Large smolt body size appears to confer a survival advantage during BYs with poor marine survival. Because early ocean growth is thought to reduce mortality from size-selective processes, large body size at ocean entry may increase survival when growth conditions during the first year at sea are poor. Overall, this research builds upon the current literature indicating that processes that occur during early marine residence are important in determining the marine survival and year-class strength of Chinook Salmon.

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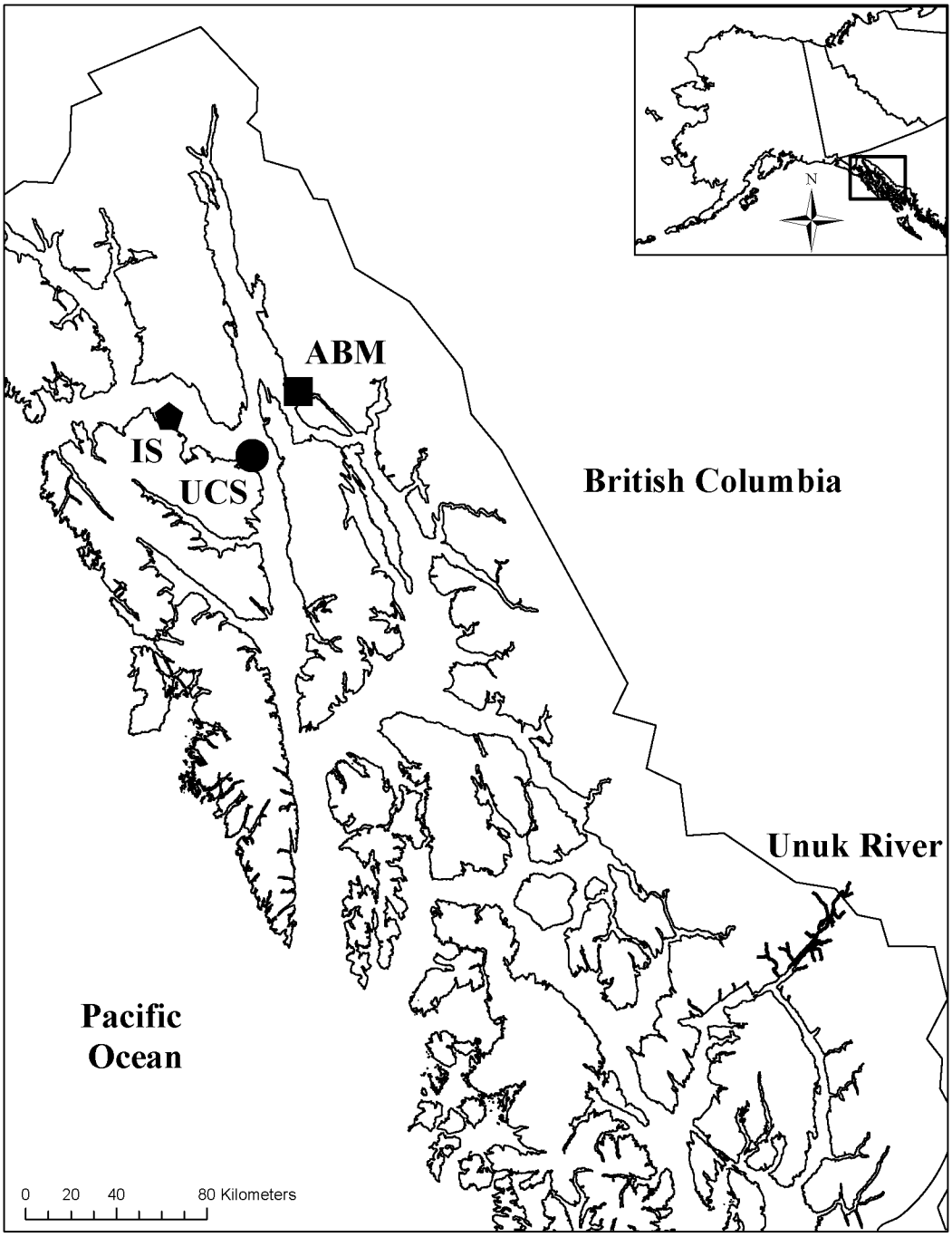

Figure 3.1. Location of the Unuk River in Southeast Alaska and British Columbia. The pentagon, square, and circles indicate the locations of Icy Strait (IS), Auke Bay Monitor (ABM), and Upper Chatham Strait (UCS) sampling locations, respectively.

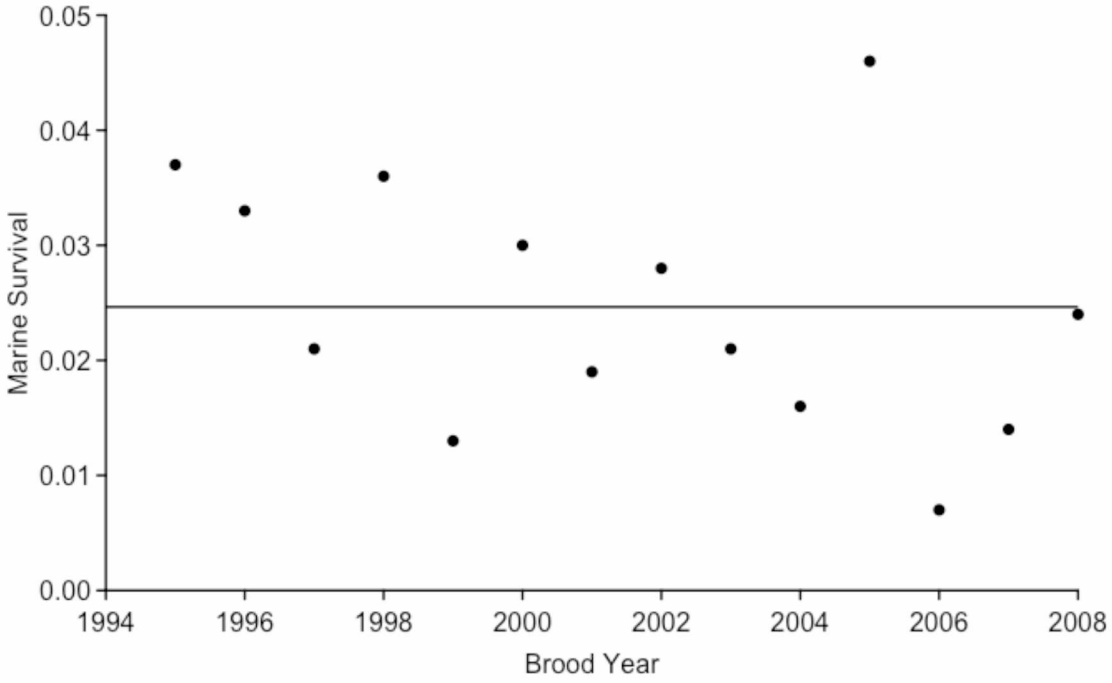

Figure 3.2. Time series of marine survival of Unuk River Chinook Salmon for brood years 1995 – 2008. The horizontal line represents the average marine survival of Unuk River Chinook Salmon for brood years 1995 – 2008.

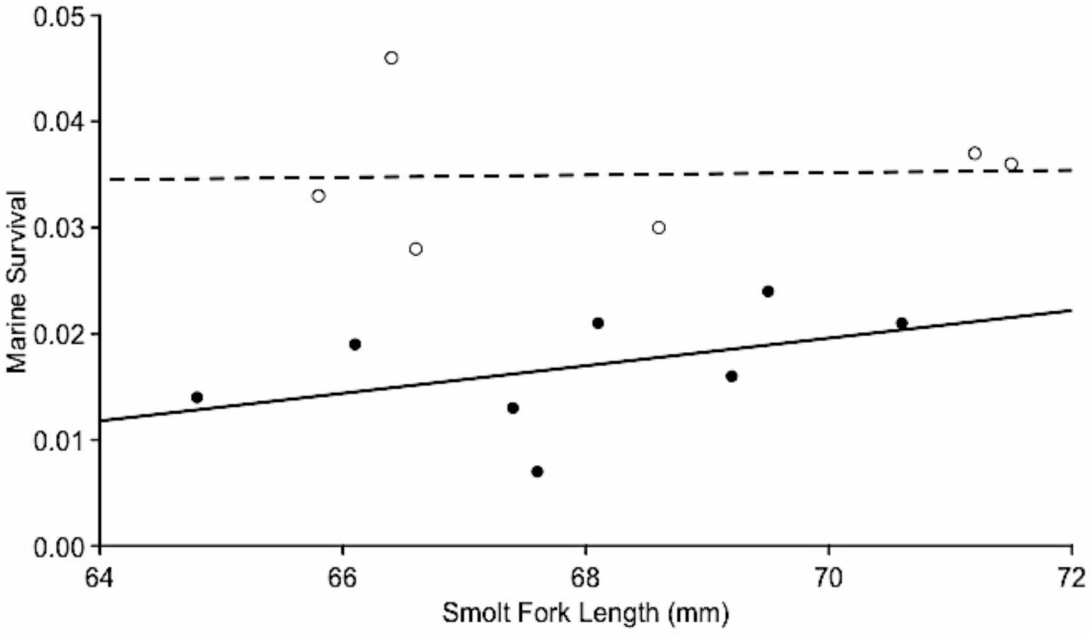

Figure 3.3. Relationship between brood year average smolt fork length and brood year marine survival for Unuk River Chinook Salmon. Open circles show brood years with above average marine survival, while solid points show brood years with below average marine survival. Lines represent simple linear regression fits using smolt fork length to explain variation in marine survival. The dashed and solid lines were taken from models that were fitted using brood years with above and below average marine survival, respectively.

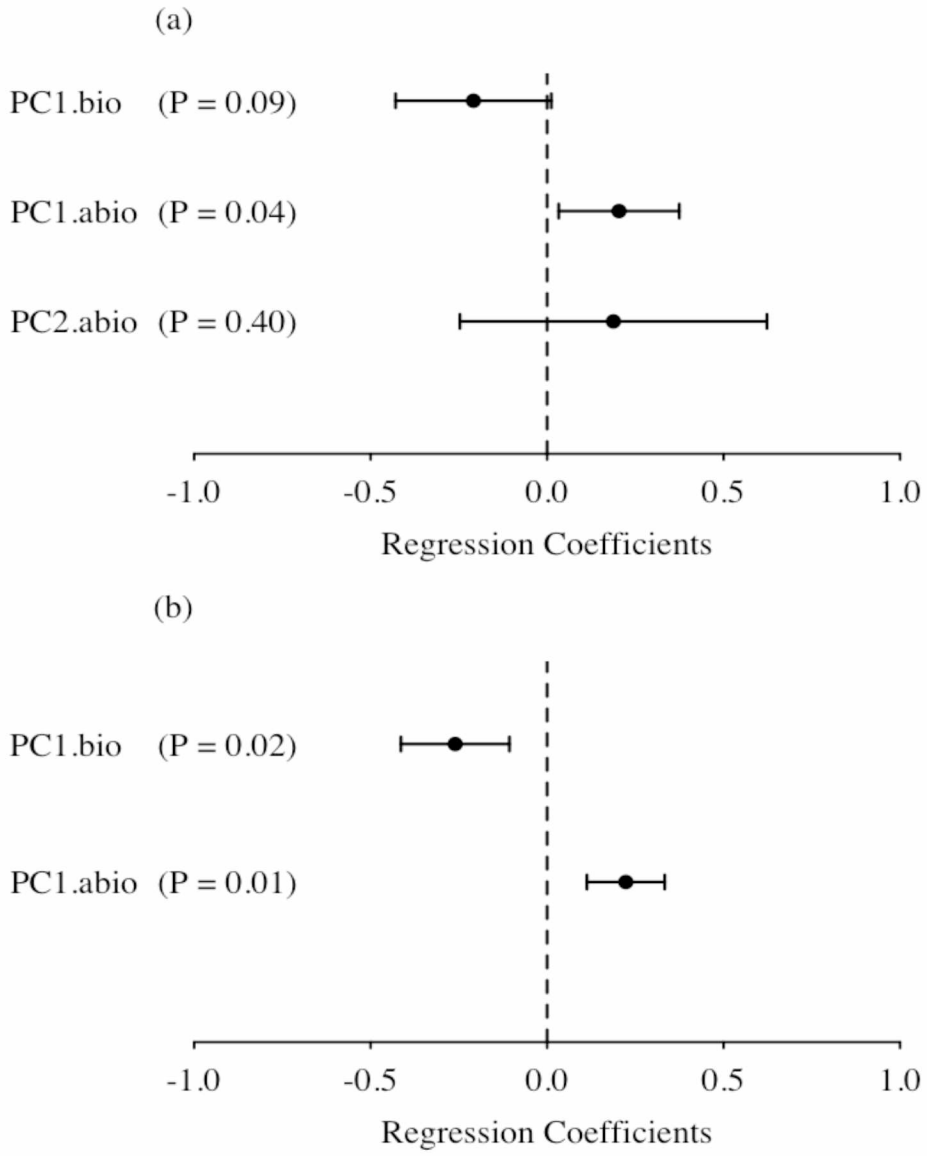

Figure 3.4. Visualization of the multiple regression models that were fitted using (a) all brood years and (b) brood years for Unuk River Chinook Salmon with below average marine survival. The retained principal components are on the y axis and estimated regression coefficients and their 95% confidence intervals are on the x axis. The dashed vertical line is at 0; confidence intervals that do not overlap with zero are statistically significant.

Table 3.1. Locations and coordinates of sample stations in Southeast Alaska. Sampling was conducted at 3 m depth by the Southeast Alaska Coastal Monitoring project (from Orsi et al. 2015).

Location	Station	Latitude	Longitude	Offshore distance (km)	Bottom depth (m)
Auke Bay Monitor	ABM	58°22.00'N	134°40.00'W	1.5	60
Upper Chatham Strait	UC1	58°04.57'N	135°00.08'W	3.2	400
Upper Chatham Strait	UC2	58°06.22'N	135°00.91'W	6.4	100
Upper Chatham Strait	UC3	58°07.95'N	135°04.00'W	6.4	100
Upper Chatham Strait	UC4	58°09.64'N	135°02.52'W	3.2	200
Icy Strait	IS1	58°13.25'N	135°31.76'W	3.2	128
Icy Strait	IS2	58°14.22'N	135°29.26'W	6.4	200
Icy Strait	IS3	58°15.28'N	135°26.65'W	6.4	200
Icy Strait	IS4	58°16.38'N	135°23.98'W	3.2	234

Table 3.2. Loadings between principal components and smolt biological variables. Proportion explained represents the proportion of total variance explained by each principal component and cumulative proportion was the cumulative proportion of variance explained.

Variable	PC1	PC2
Smolt length	-0.71	-0.71
Smolt weight	-0.71	0.71
Proportion explained	0.92	0.08
Cumulative proportion	0.92	1.00

Table 3.3. Loadings between rotated principal components and Auke Bay Monitor (ABM), Upper Chatham Strait (UCS), Icy Strait (IS) sea-surface temperatures. Proportion explained represents the proportion of total variance explained by each principal component and cumulative proportion was the cumulative proportion of variance explained.

Variable	PC1	PC2	PC3
ABM	0.53	-0.85	0.02
UCS	0.60	0.36	-0.71
IS	0.60	0.39	0.70
Proportion explained	0.84	0.14	0.02
Cumulative proportion	0.84	0.98	1.00

General Conclusions

The results of my study increased our understanding of how biotic and abiotic factors influence the survival and production of Chinook Salmon stocks in Southeast Alaska (SEAK). In the first chapter, I characterized the importance of annual growth in determining the recruitment success of two regionally important salmon stocks in SEAK. Growth during the first year at sea was positively related to marine survival and total return of both stocks while growth during the third year at sea was positively related to the survival of Taku River Chinook Salmon. In addition, I found evidence of growth dependency in Taku River Chinook Salmon and that both stocks experienced size-selective mortality at ocean entry. In the second chapter, I examined the influence of abiotic and biotic factors on the freshwater overwinter survival and smolt production of Unuk River Chinook Salmon and found that high spring temperatures and high fall and spring discharges may have a negative effect on smolt production within the system. In my third chapter, I examined the relative influence of smolt body size and regional sea-surface temperatures in determining the marine survival of Unuk River Chinook Salmon. There was a consistent positive relationship between sea-surface temperatures in Icy Strait, Upper Chatham Strait, and Auke Bay Monitor during early marine residence and Chinook Salmon marine survival. In contrast, large smolt body size only provided a survival advantage during years with below average recruitment success.

Chinook Salmon are highly valued and support important sport, commercial, and subsistence fisheries in SEAK. Recent declines in the survival and productivity of Chinook Salmon stocks across the region have prompted research focused on identifying the cause of these declines (ADF&G Chinook Salmon Research Team 2013). Previous research suggests that

salmon abundance is mediated by size-dependent mortality, with the time period during freshwater and early marine residence being critical for influencing survival patterns and, ultimately, recruitment to the spawning stock (Holtby et al. 1990; Mortensen et al. 2000; Beamish and Mahnken 2001; Mueter et al. 2002; Tomaro et al. 2012; Murphy et al. 2013; Miller et al. 2014; Murphy et al. 2016) Therefore, growth is thought to be a crucial determinant of recruitment strength (Beamish et al. 2004); however, the relative importance of freshwater versus marine growth in determining recruitment success Chinook Salmon stocks in SEAK was uncertain. My research confirmed that early marine processes influence the recruitment success of Chinook Salmon in SEAK, with high growth during the first year at sea being associated with increased survival and run sizes for both stocks. In addition, growth during freshwater residence (i.e., smolt body size) had a negligible impact on the recruitment success of either stock. These findings are congruent with other research that indicates growth during early marine residence explains more variation in the survival rates of Chinook Salmon than does size-at-marine entry (Duffy and Beauchamp 2011; Tomaro et al. 2012; Miller et al. 2014). While freshwater scale growth was not related to survival or returns for either stock, the results of my research suggest that growth during freshwater residence may influence survival patterns. There was a positive relationship between freshwater and first year marine growth for individual Chinook Salmon from the Taku River. High growth during freshwater residence may allow Chinook Salmon to transition to a fish-based diet earlier in their marine residence, thereby increasing growth rates, and potentially survival of individual fish. In addition, because both stocks experienced size-selective mortality at ocean entry, high growth during freshwater residence may reduce mortality during early ocean residence. Finally, large smolt body size may provide a survival advantage for brood years that experience poor growth conditions during their early marine residence.

The importance of growth in influencing the recruitment success of both stocks suggests that the current declines in the spawning run sizes of stocks across the region may be attributed to poor growth conditions or poor growth during the first year at sea. Unfortunately, the processes that regulate growth of Pacific salmon in SEAK are not well understood. Climate may influence the growth and survival of Pacific directly through changes in metabolism and indirectly through changes in prey quality and the trophic structure of ecosystems (Mueter et al. 2002; Peterson and Schwing 2003). My research demonstrated that regional sea-surface temperatures during early marine residence were positively correlated with the marine survival of Unuk River Chinook Salmon. This suggests that warm sea-surface temperatures in the corridor near Upper Chatham Strait, Icy Strait, and Auke Bay Monitor in SEAK may promote growth, either directly or indirectly, which in turn, would increase survival by limiting the amount of time Chinook Salmon spend in size classes that are vulnerable to predation (Sogard 1997). Future research should focus on identifying the biotic and abiotic factors that influence growth during the first year at sea to elucidate the mechanisms that link climate to survival in Chinook Salmon stocks in SEAK.

The results of my first and third chapters indicated that biotic and abiotic processes during the first year at sea influence the survival of Chinook Salmon in SEAK; however, my research was not able to identify the timing of mortality. One way to identify the timing of this mortality would be to sample Chinook Salmon throughout their first marine year and compare length-frequency distributions between sampling periods; positive shifts in these distributions between sampling periods would indicate the timing of size-selective mortality. Identifying the timing of mortality is important because if brood-year recruitment strength is determined during this period, managers may be able to use juvenile abundance estimates after this period to

forecast adult returns within the region (Murphy et al. 2016).

One unexpected result of my research was the positive relationship between third-year marine growth and survival of Taku River Chinook Salmon. This finding is counter to the prevailing paradigm that size-selective processes during freshwater and early marine residence determine the recruitment strength of Pacific salmon and suggests that Chinook Salmon are susceptible to size-mediated morality later in their life history. While the marine overwintering period is thought to be physiologically stressful and may result in depleted energy reserves and starvation-induced mortality (Beamish and Mahnken 2001), Chinook Salmon should have attained a sufficient body size by their third marine year that would make this type of mortality unlikely. Current research indicates that large-bodied Chinook Salmon experience predation by both homeothermic and poikilothermic predators in the Bering Sea and Gulf of Alaska (M. Courtney, University of Alaska Fairbanks, personal communication). In contrast to Unuk River Chinook Salmon that primarily rear in inside waters near SEAK during their marine residence, Taku River Chinook Salmon rear in the Gulf of Alaska and Bering Sea. Therefore, high growth during the third year at sea may make Taku River Chinook Salmon less susceptible to predation-based mortality from Salmon Sharks *Lamna ditropis* and Killer Whales *Orcinus orca* while they inhabit the Gulf of Alaska and Bering Sea (Nagasawa 1998; Ford and Ellis 2006).

Freshwater systems in SEAK may be impacted by both climate change and proposed development. Southeast Alaska is thought to be sensitive to climate change due to its near freezing winter air temperatures (i.e., -4 ^{o}C; Shanley and Albert 2014). Therefore, small changes in air temperatures may transform freshwater systems from glacially and snow-fed systems to rain-fed systems. These changes may result in altered flow patterns and temperature profiles, which in turn, may influence survival rates of Chinook Salmon. The results of my research

suggest that anticipated increases in fall and spring discharge due to climate change may result in lower smolt production within the region. In addition to climate change, proposed transboundary open-pit mines on both systems threaten pristine spawning and rearing habitat. One concern associated with open-pit mining is increased selenium levels in watersheds, which may reduce the growth and survival of fishes (Hamilton et al. 1990). My research provided important baseline data relating to freshwater growth in both systems that may be used to assess the impact of climate change and regional development on the freshwater growth rates of Chinook Salmon in these systems.

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